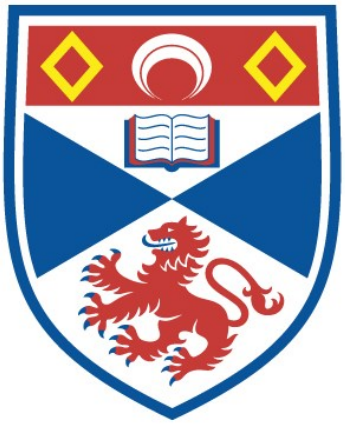
NEUROETHOLOGICAL STUDIES OF PRIMATE SOCIAL PERCEPTION

Nathan J. Emery

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews

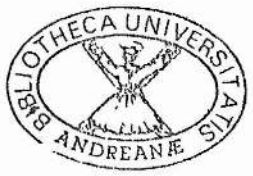


1997

NEUROETHOLOGICAL STUDIES OF PRIMATE SOCIAL PERCEPTION

Nathan J. Emery

June 1997



A thesis submitted to the University of St Andrews for the degree of Doctor of Philosophy in the School of Psychology.

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

This thesis is dedicated in loving memory to my grandmother

Doreen Emery
(1922-1996)

DECLARATION FOR THE DEGREE OF PhD.

I, Nathan Jon Emery, hereby certify that this thesis, which is approximately 90,000 words in length, has been written by me, that it is a record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

date 24/9/97 signature of candidate .....

I was admitted as a research student in January 1994 and as a candidate for the degree of Doctor of Philosophy in January 1994; the higher study for which this is a record was carried out in the University of St Andrews between 1994 and 1997.

date 24/9/97 signature of candidate .....

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

date 24/9/97 signature of supervisor .....

THESIS COPYRIGHT DECLARATION

Unrestricted

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker.

date 24/9/97 signature of candidate .....

Acknowledgements

One of my greatest debts of gratitude has to go to my supervisor, Dave Perrett. There is no denying that Dave is a difficult task-master and extremely infuriating at times, but without his enthusiasm and encouragement for my work (a lot of it which was new to him), I would not have completed. I also thank Dave for teaching me the right way to do research; to try and enjoy it!

The work reported in this thesis would not have been possible without the help of a large number of people. Electrophysiology is a physically and mentally tiring way to spend an afternoon and the results herein would not have been possible without help from many people. My thanks go to Mike Oram for teaching me physiology and Lisi Wachsmuth, Chris Baker and Erika Lorincz for sharing some of the joys and hardships of physiological recording. I would also like to thank Mike for discussions of many of the issues raised in this thesis (and some not so academic) and for stats help and Erika for help with the behavioural experiment.

I would also like to thank the technical staff for their essential help. The animal tehnicians, Hilda Dickie, Wendy Taylor, Heather Bowman and Jo Hutchison, for unsurpassed care of the animals and the workshop technicians, Brian Kirk, Pete Wilcox, Malcolm McCandless and Andy Burnley for audio-visual, carpentry, computer and electronics wizardry. I would also like to thank Mary Latimer for making electrodes and help with histology. The secretaries, Lesley Ferrier, Vanessa Shepherd, Sandra Scott and Julie Anderson never get the thanks they deserve. They will do anything for you at the drop of a hat and there have been a million times where their help has been vital. I cannot thank them enough.

The Biotechnology and Biological Sciences Research Council (BBSRC) provided grant and travel support, and I am particularly thankful that they gave me a life-saving extension to my grant for the last 6 months. The writing of this thesis would have been very difficult without those funds. I'd also like to thank the journal *Brain*, the School of Psychology, University of St Andrews, the Experimental Psychology Society and the European Neuroscience Association for travel grants.

The main thing that has kept me on track has been my many friends. I have been extremely fortunate to have so many supportive, funny and downright wierd friends, throughout the whole of my PhD. In particular, I'd like to thank Penny and Glenda (my landladies), Julie, Dave C, Duncan R, Mike, Alison, Kev, Lindsey, Sasha, Rebecca and Emma, and especially my "golf buddies", Rob, Ed, Ken and Duncan C. I'd also like to thank Chris, Ian, Catrin, David D, Jonathan, Paul and Linda (Gardner, not McCartney), Jeremy, Laura, Vince, Clea and Stacy.

Malcolm Young and Gully Burns provided assistance with the NMDS analysis and Rob Barton provided last minute assistance with the CAIC analysis and useful discussions about comparative anatomical analyses. Dick Byrne, Juan Carlos Gomez, Eric Bowman, Dave Carey, Verity Brown and Andy Whiten all provided references and books for loan without complaint.

This thesis would not be possible without Steve, Esther and Terry, my subjects and my heartfelt appreciation goes to them.

Finally, I would like to thank my family, my mum and dad and my brother, Damon who have encouraged me in everything I have done. They have always been there for me, with support, money (!) and someone to talk to. Both sets of grandparents have been wonderful in their support and it is for this reason that I dedicate this thesis to my late grandmother. Everybody says this, but I definately have the best parents in the world. They are my best friends, and I love them dearly (and don't tell them enough). If this thesis was dependent on anything, it was their love and encouragement.

Abstract

The neuroethological basis of social signals was investigated using a multidisciplinary approach, involving connectional and comparative analysis of anatomical data, single cell recording and behavioural techniques. Previous literature implicates the amygdala, anterior temporal and prefrontal cortex in primate social functions. Non-metric multidimensional scaling (NMDS) and cluster analysis were used to analyse the connectional relatedness of macaque cortico-cortical and amygdalo-cortical connections. This objective analysis separated the amygdala nuclei into two groups, the basolateral (BL) and centromedial (CM) complexes. A comparative analysis was made of the possible functions of the amygdala nuclei by correlating amygdala nuclear volume with 5 socio-ecological indices, across 44 primate species. The lateral basal (LB) nucleus and BL size was found to correlate positively with social complexity. CM size correlated negatively. The LB nucleus receives information from the STS, which contains visual neurons responsive to eyes, heads and bodies. These cells were assessed for coding of socially relevant information. Single cell recording localised within the macaque superior temporal sulcus (STS) revealed neurons responsive to specific views, elevations and orientations of the head, eye position, specific views of bodies walking in specific directions and reaching to objects. The tuning of these neurons could therefore support the function of recognition of another's purposive behaviour (e.g. direction of attention or intention). Visually responsive neurons in the STS also differentiated faces of different species (i.e. monkeys, humans and other animals). Behavioural studies suggest that monkeys do not follow the direction of attention of humans, yet monkeys appear to have the neural capacity. A behavioural study using video stimuli, revealed that monkeys spontaneously follow other monkeys' gaze onto an object or point in space. It is concluded that the amygdala and STS are part of a neural system which enable monkeys to interpret another's gaze and actions within a purposive behavioural framework.

TABLE OF CONTENTS

TABLE OF ILLUSTRATIONS

Figures

Tables

Chapter I

General Introduction

"Although in practice we cannot, of course, collect data on every relevant aspect of an animal's biology, we do need to be aware that concentrating on one issue to the exclusion of all others is to risk doing no more than tinkering with Nature. It is a bit like trying to understand how a car works simply by fiddling with the carburettor."

Dunbar (1988, p. 5)

1.0 Background to study

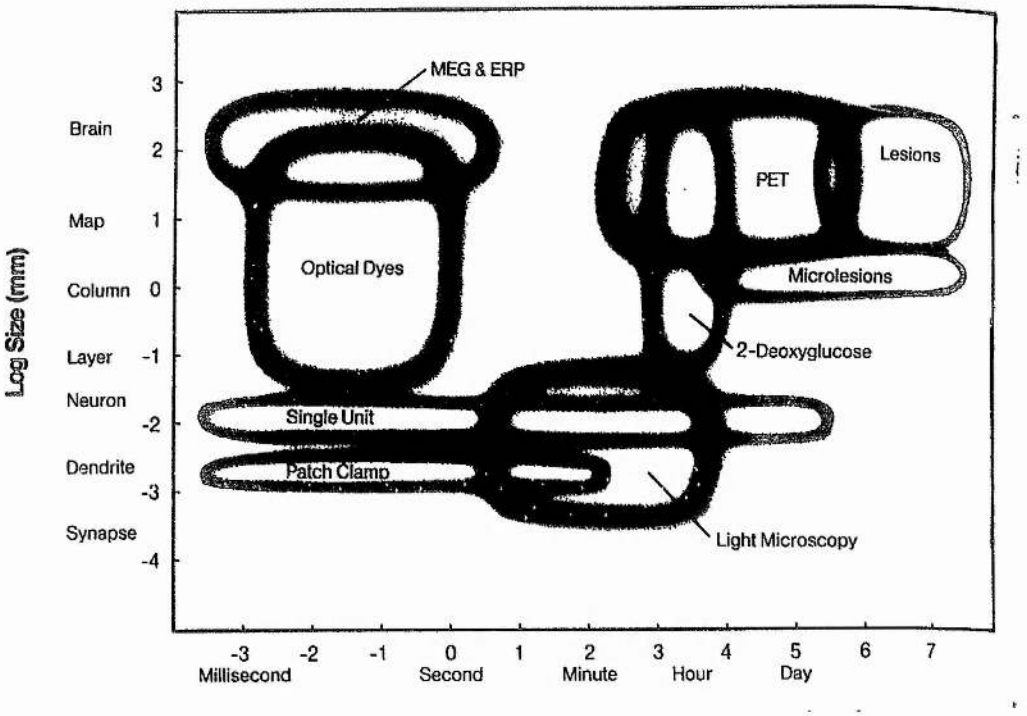
The experiments presented in this thesis were designed primarily to determine the role of the temporal cortex of the macaque in coding aspects of visual social communication, such as the perception of social signals. Over 100 years of research, beginning with Brown and Shafer (1888) have revealed how different areas of the brain function in recognising and controlling aspects of social behaviour in human and non-human primates. During this time, three areas of the brain have been proposed to perform such functions; the anterior temporal cortex, the amygdala and the prefrontal cortex. This thesis will show that there are good anatomical reasons for these three areas to be so heavily involved in social processes. It must be stressed however, that the brain and body act as a whole in all forms of social behaviour. The neuroendocrine system controls hormone levels; cortisol and adrenal levels in times of social stress, testosterone and oestrogen levels during sexual behaviour, and levels of oxytocin and prolactin to provide adequate milk during child-rearing. The visual system enables recognition of the different individuals performing in a social interaction, the hippocampus and ventral temporal cortex aid in remembering previous interactions and the motor system produces the external response behaviour.

1.1 Reasons for study and the techniques used

There have been over 100 years of research in this area, but the precise functions of the above brain regions are still very sketchy. Linking a discreet physiological event with its associated behaviour is one of the most important areas of modern psychological and neuroscientific research. Relating a precise physiological event to an exact anatomical location can only be performed using two different methodologies. Event-related potentials provide useful temporal information concerning the onset and continuation of a stimulus, but spatial localisation of function is very poor. The new imaging techniques, such as Positron Emission Tomography (PET) and Magnetic Resonance Imaging (MRI) are examples of the new importance of relating function with structure. Many brain scientists (psychologists and neuroscientists) have jumped on the neuroimaging band-wagon and have feverishly applauded the arrival of these techniques, but there are inherent difficulties associated with using this methodology. One reason for the furore concerning PET and MRI was from the animal rights movement. All research must be for the ultimate good of humans, and a technology that would reduce or halt altogether the need for brain research on animals would be seen as a step forward. Unfortunately, only a few research questions can be answered using these techniques, and the answers need to be analysed properly. Particular concerns are that temporal information is unreliable due to the length it takes to collect reliable data, and function can only be resolved at fairly gross levels, dependent on the statistical probability levels of the investigating team. Questions relating to animals are difficult, if not impossible to answer using neuroimaging techniques, without anaesthetising the subjects. Anaesthetising subjects removes at least 90% of the questions you would want to ask using PET and MRI.

Physiology is still the method of choice when good temporal and spatial resolution is required (see Figure 1.1). The relatively new field of primate neuroethology is beginning to make progress in finding links between small distinct events at the single-cell level and higher forms of visual and motor behaviour.

Figure 1.1. Diagrammatic representation of the spatial and temporal characteristics of a variety of neuroscientific methods. The y-axis displays the spatial resolution of the methods employed. The x-axis displays the possible lengths of time with which the individual methods may be used. For example, single-unit physiological recording has very good spatial resolution (single cell), and good temporal reolution (millisecond accuracy and can be used continuously for many days). ERP's have very good temporal resolution (milliseconds to seconds), but poor spatial resolution (large brain region to whole brain).



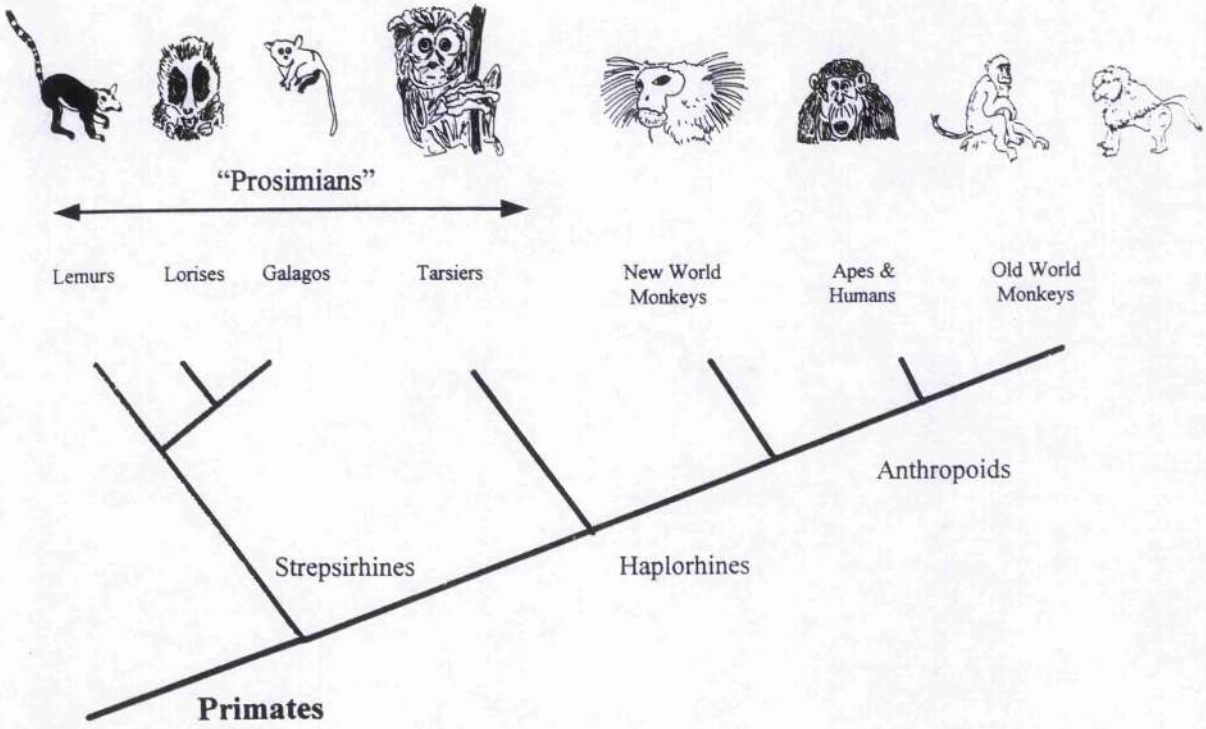
1.2 Why use the rhesus macaque?

There are three important reasons for using *Macaca mulatta* as a subject in the experiments reported in this thesis. The rhesus monkey is an extremely social animal. It would be futile to attempt a study of the neural basis of social behaviour if the experimental subject lived a solitary existence in it's natural environment. As will be discussed in Chapter II, the rhesus monkey lives in very large social groups, with defined dominance hierarchies, and complex forms of social communication, such as vocalisations and facial expressions. Rhesus monkeys are also highly visual animals. They are alert, have colour vision similar to humans, and use a wide range of facial expressions, postures, gestures and other visual social signals in their communication. The plethora of knowledge on the dynamics of rhesus monkey social behaviour is essential to this study.

The physiology and anatomy of the rhesus monkey brain, and in particular the neocortex has been extensively mapped. Knowledge of the monkey brain's anatomical connectivity, neurochemistry and electrophysiological properties of cells is extensive. Part of this knowledge has been gained with the express reason that the macaque monkey is the only commonly used experimental animal which is phylogenetically close to humans (see Figure 1.2 for cladisitic diagram of primate phylogeny). Our closest living relatives, chimpanzees are not used comprehensively for research, and not at all for basic neuroscience research. Many quarters believe that using the great apes purely for research purposes is unethical for the reason that they are genetically close to humans.

Neurophysiological and behavioural methods have been successfully used in rhesus macaques for over 40 years. These methods are well known throughout the neuroscience community and have been extensively developed. As an experimental animal, the rhesus monkey is relatively easy to look after when compared to other experimental primates. They are hardy animals, being extremely resistant to disease. Rhesus monkeys are also highly intelligent and can be trained to perform a wide variety of perceptual and cognitive tasks which are incorporated into the neurophysiology and behaviour experiments.

Figure 1.2. Diagrammatic representation of the phylogeny of the primate order, including prosimians, Old and New World monkey, lesser and great apes. The lengths of the branches (on the "primate family tree") are approximations of lengths of biological time since the presence a common ancestor to two extant species, derived from molecular biological studies (Waddell and Penny 1996). For example, the common ancestor to common chimpanzees (*Pan troglodytes*) and bonobo chimpanzees (*Pan paniscus*) was living 2.0 - 2.5 My ago (see Byrne 1995).



1.3 Justification for the multi-disciplinary approach

This thesis is a little unusual in that it incorporates data from four main areas; connectional anatomy, behaviour, neurophysiology and evolution. The empirical data from the behavioural and neurophysiological experiments are new, whereas the data from the connections and evolutionary anatomy experiments were derived from previously published sources. It is justifiable to use such sources when the data is re-analysed or analysed in different ways from the original sources.

In science there appears to be a general trend in collecting data for data's sake. These data are then used either as the basis for research closely related to the original research, forgotten or written up as part of a review. Data should be published so that it can be used to help answer the questions of many researchers. Anatomy is one subject which appears to "rest on it's laurels" and not use data which has taken years, vast expense and a large number of animals to collect. The basic premise of anatomy is to discover whether area X connects to area Y. This in itself is valuable information, but more can be done with this data. A new method will be described in chapter IV which uses a systems level approach to look at how connectional anatomy can ask questions of neural organisation, gross brain structure and behaviour.

Questions are rarely asked as to how a certain behaviour or brain region has evolved. It may seem common sense that two closely related species with similar brain structures would also have similar behavioural repertoires. The liver, for example, performs the same function in closely related species, but does the brain and behaviour also perform the same or similar functions in closely related species. The comparative method (Harvey and Pagel 1991) allows the evolutionary analysis of behavioural and anatomical traits to determine whether a basic assumption is true for a complete set of data. In chapter V, the results of the connectional systems analysis allow further questions to be developed about how social behaviour is coded and whether the neural coding of this behaviour can be localised at a relatively gross level.

1.4 Thesis overview

Chapter II reviews three areas of investigation; primate social behaviour and cognition, brain coding of social behaviour and human social cognition deficits after brain assault or psychopathology. The first section describes studies of visual social communication from three areas, primates observed in the field, behavioural studies of captive primates and experimental studies performed in the laboratory. The second section describes the history of studies attempting to relate non-human primate social communication to specific brain structures, such as the amygdala, temporal and prefrontal cortices. The final section complements the first two sections by first discussing aspects human social cognition and the so-called theory of mind mechanism. It then discusses how specific brain lesions or psychopathology such as autism and schizophrenia can also cause deficits in human social cognition. These deficits will be assessed and compared with those seen in non-human primates.

Chapter III briefly reviews the anatomy and connectivity of the amygdala and superior temporal sulcus, two brain regions said to be primarily involved in recognition of social signals, as highlighted in Chapter II.

The connections of the amygdala and superior temporal sulcus are analysed using a novel method in Chapter IV, using published details of connections to determine whether the connection patterns of these areas are related to their probable function. Chapter V further tests the validity of the data derived in Chapter IV by testing the hypothesis that the amygdala (and the component parts of the amygdala) have different functional roles to play in primate social behaviour, and these role have changed throughout primate evolution. These hypotheses were tested using comparative anatomical and socio-ecological data of prosimian and simian primate species from the literature.

Chapter VI contains details of all the neurophysiological methodology used in collecting the data for Chapters VII and VIII.

Chapter VII is the first of the empirical physiology chapters. An individual needs to recognise in which direction another individual is attending or moving to and which object it is attending to or interacting with. Such simple calculations are essential

precursors for some higher aspects of social cognition, such as determining others' intentions and predicting their subsequent behaviour. The basic physiology of neurons in the recorded areas of the anterior temporal cortex and superior temporal sulcus (STS) are also reported.

Chapter VIII is the second empirical physiology chapter. One important aspect of social perception that is often overlooked is how an individual recognises a face of the same species when all faces have the same basic configuration (two eyes, nose in the centre, mouth underneath, two ears to the sides, etc.). Cells responsive to different and similar animal species are reported.

Chapter IX looks at one aspect of human and non-human primate social perception and cognition; the recognition and use of gaze. This chapter details a behavioural experiment studying this form of behaviour in two rhesus macaques, and discusses similar abilities across other species. The results of this final empirical chapter bring together the results of the previous chapters, by proposing that processing others' gaze may be dependent on neural systems in the superior temporal sulcus and amygdala.

Chapter II

Primate Social Neuroethology

a literature review

"the study of visual signals may eventually provide an insight into how primates think"

Zeller (1987, p. 439)

"All I need to do is to be alert to those moments when another living being shows signs of emotion or interest. It will not be long before I discover the things which seem to be important to him, not because he has communicated them to me by language, but because I myself have observed and remembered them....a signal without an intrinsic content may acquire meaning in my mind by what I observe at the time. The ability that two living beings have to pick out the moments of each other's special, active attention is itself a language....social animals may have an active, intelligent, flexible means of communication long before the development of language and even without any code of common signals."

Wiener (quoted in Menzel 1971, p. 221)

2.0 Introduction

One of the traits that separate primates from other mammals is the advanced form of social behaviour they employ. This is especially true for *Homo sapiens*. That is not to say that other mammals (such as rodents, carnivores, etc.) do not use elaborate forms of social behaviour (Packer and Ruttan 1988). Indeed, some carnivore and rodent species possess groups comprising more individuals than those seen in many primate social

groups. The difference between primates and non-primate mammals is the complexity of their social behaviour or social cognition. The primate brain has evolved radically in complexity when compared to other mammals and the increased intricacy of social living may have induced this (Humphrey 1976, Byrne and Whiten 1988).

The form and function of social communication in primates is ultimately more complicated than seen in other mammals, whatever sensory channel is used; auditory, visual, olfactory or tactile. An important aspect of social communication (in any animal) is the recognition, use and production of social signals. For a social signal to function correctly it must a) be directed at a particular recipient or recipients, b) provide some form of information, and c) have an adaptive value.

The modality of signal preferred by a given species is wholly dependent on 1) the environment in which they live (arboreal or terrestrial), 2) their lifestyle (nocturnal or diurnal), 3) group social structure, 4) predation risk, 5) body morphology (correct apparatus for producing and receiving social signals) and 6) brain structures adapted for producing and comprehending signals. For example, capuchin monkeys live a largely arboreal lifestyle, with low predation risk and relatively large stable groups. Language would be an ideal form of communication for these primates, however, they lack the appropriate neural (Broca's and Wernicke's areas, amongst others) and morphological structures (malleable lips and vocal tract) required for language to be selected as a form of communication. This is an extreme example, but it highlights the fact that a number (or all) of points 1 to 6 need to be present before a certain form of communication can evolve. The costs and benefits of each mode of communication is evaluated in Table 2.1.

Anthropoid monkeys and apes are mainly terrestrial living primates and because of this, use visual communication above all other forms of communication (perhaps with the exception of auditory/vocal communication). The rhesus monkey (the main subject of this thesis) uses primarily visual communication. This chapter discusses ethological, behavioural and neurobiological studies of recognition, comprehension and production of visual signals for social communication, in human and non-human primates.

Table 2.1. Cost and benefits of different methods of primate communication. The different modality used to transmit information is described as well as the costs and benefits of using the method of communication.

Modality	Costs	Benefits
Olfactory	-Imprecise as to the recipient (information may be received by a large number of conspecifics or predators) -Slow acting	- Can be transmitted over long distances - Not constrained by light levels - Can be individualised (e.g. specific scents) - Can be used to communicate over time (e.g. scent-marking territory)
Auditory	- Imprecise as to the recipient (information may be heard by a large number of conspecifics or predators) - Cannot be used to transmit information over time (however, language?)	- Fast - Can be transmitted over long distances - Not constrained by light levels - Can be individualised - Can be used to transmit large amounts of different types of information - Can be used to communicate about the presence of objects and events
Tactile	- Constrained by length of limbs (i.e. cannot be used to communicate over long distances) - Relatively short acting - Limited in the forms of information which can be communicated	- Precise as to the recipient - Can be used to communicate specific information - Not constrained by light levels
Visual	- Constrained by light levels - Bright colours can alert other conspecifics or predators	- Precise as to the recipient - Can be used to transmit information over time (e.g. individual recognition or sexual swellings) - Can be used to transmit large amounts of different types of information - Can be used to communicate about the presence of objects and events -Fast

2.1 Primate Social Behaviour & Communication

2.1.1 What is social communication?

It is appropriate to describe what social communication is before discussing the role that visual signals may play in this form of behaviour. This may appear to be simple to answer, but this very question has caused debate and controversy for behavioural biologists, neuroscientists, linguists, psychologists and anthropologists alike. A working definition of social communication would be advantageous at this stage of the review, but discussions of the history of the term communication will not be discussed here as they have been dealt with in much more detail and with finer clarity elsewhere (Marler 1977, Krebs and Dawkins 1984, Dawkins 1987, Gomez 1994, Hauser 1996).

Dawkins' (1981) definition of communication will be used here; "Animal A is said to have communicated with B when A's behaviour manipulates B's sense organs in such a way that B's behaviour is changed (pp. 79)." Cheney and Seyfarth's work on vervet alarm calls (1990a), provides an example of this. Vervet A gives an alarm call to vervet B, and vervet B runs into the trees, looks down to the ground, or runs into the bushes, depending on the precise nature of the call given. Vervet B's behaviour has been changed by vervet A's behaviour (alarm call). Dawkin's definition is useful in this context, as there is an emphasis on the function of communication changes, from reflexive and involuntary to volitional and intentional. The underlying function of communication does not change. It may be added that information of some sort is communicated when Animal A changes Animal B's behaviour, or this may be the underlying reason why animal B's behaviour changes (as a consequence of that information). The information transmitted could take one of many forms, such as an alarm call notifying others of the presence of a predator, or the emitter's emotional state concerning that predators proximity, a facial expression of threat, a pheromone signalling sexual receptivity, or sentences transmitting gossip about an unseen third party.

2.1.2 Morphological and ecological constraints on visual social communication

This section will discuss the morphological and environmental changes which would have enabled certain uses of visual communication to be selected for over others. It is viable to use such information to discuss behaviour in similar ways as paleoanthropologists trying to discuss the behaviour of extinct hominids from fossil remains, geological and environmental data and archaeological artefacts (Mithen 1996).

The morphology of the primate face has changed dramatically from prosimians to New World monkeys (e.g. squirrel and capuchin monkeys), Old World monkeys (e.g. baboons and macaque monkeys), lesser apes (e.g. gibbons and siamangs) and the great apes (e.g. orangutans, gorillas, chimpanzees and humans). Figure 2.1 shows the proposed evolutionary history of the primates and how the primate faces differ between species. There is a diverse range of inter-group differences in facial anatomy; the small face of the loris with the proportionally large forward facing eyes, the long snout of the ring-tailed lemur, the dog-face of the hamadryas baboon, the prominent nasal features of the proboscis monkey, the malleable lips of the chimpanzee and the large throat pouches of the adult male orangutan, as a collection of examples (Jolly 1972).

What should be clear from any discussion of the evolution of external facial morphology is the reduction in the protrusion of the face from monkeys to apes, in particular, the reduction in jaw size and length of the snout or nose. All the great apes, including humans have relatively flat faces whilst retaining some prominent features. For example, the human face has high cheekbones, a conspicuous nose and eyebrows framing the eyes. Such features could all function to highlight the region around the eyes (the eye brows), moving the eyes (the cheekbones and musculature) or directing attention to the eyes (the nose). For example, these changes may have provided a shift in emphasis from the shape of the face (and it's orientation) to the eyes as sources of information about attention direction. Determining the direction of another's attention is easier to establish from larger visual cues, such as the head. Flattening the face of the great apes could have reduced the amount of information that could be transmitted by the head alone. The eyes

Figure 2.1. Drawings displaying the range of diversity of primate faces, including **(a)** ring-tailed lemur (*Lemur catta*), **(b)** aye-aye (*Daubentonia madagascariensis*), **(c)** common marmoset (*Callithrix jacchus*), **(d)** olive baboon (*Papio anubis*) **(e)** capuchin monkey (*Cebus apella*), **(f)** Japanese macaque (*Macaca fuscata*), **(g)** whitehanded gibbon (*Hylobates lar*), **(h)** orangutan (*Pongo pygmaeus*), **(i)** gorilla (*Gorilla gorilla*), **(j)** bonobo (*Pan paniscus*) and **(k)** human (*Homo sapiens*).

(a)

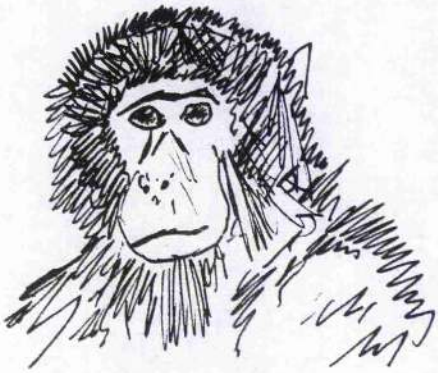
(b)

(c)

(d)

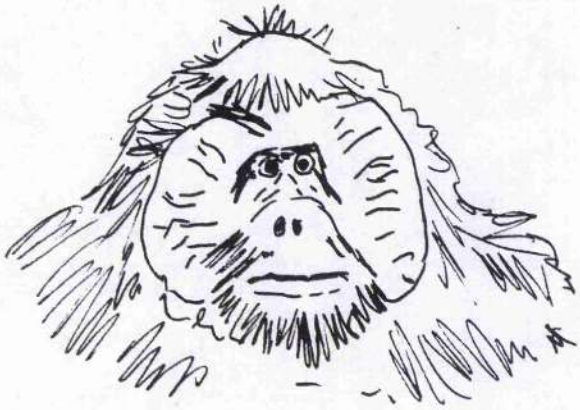
(e)

(f)



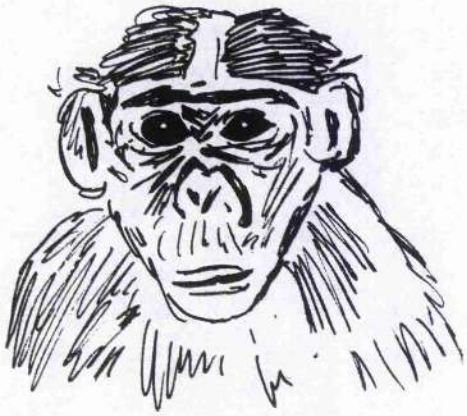
(g)

(h)



(i)

(j)



(k)

are much smaller than the head, but they present a more precise indicator of where another is looking (see Chapter IX).

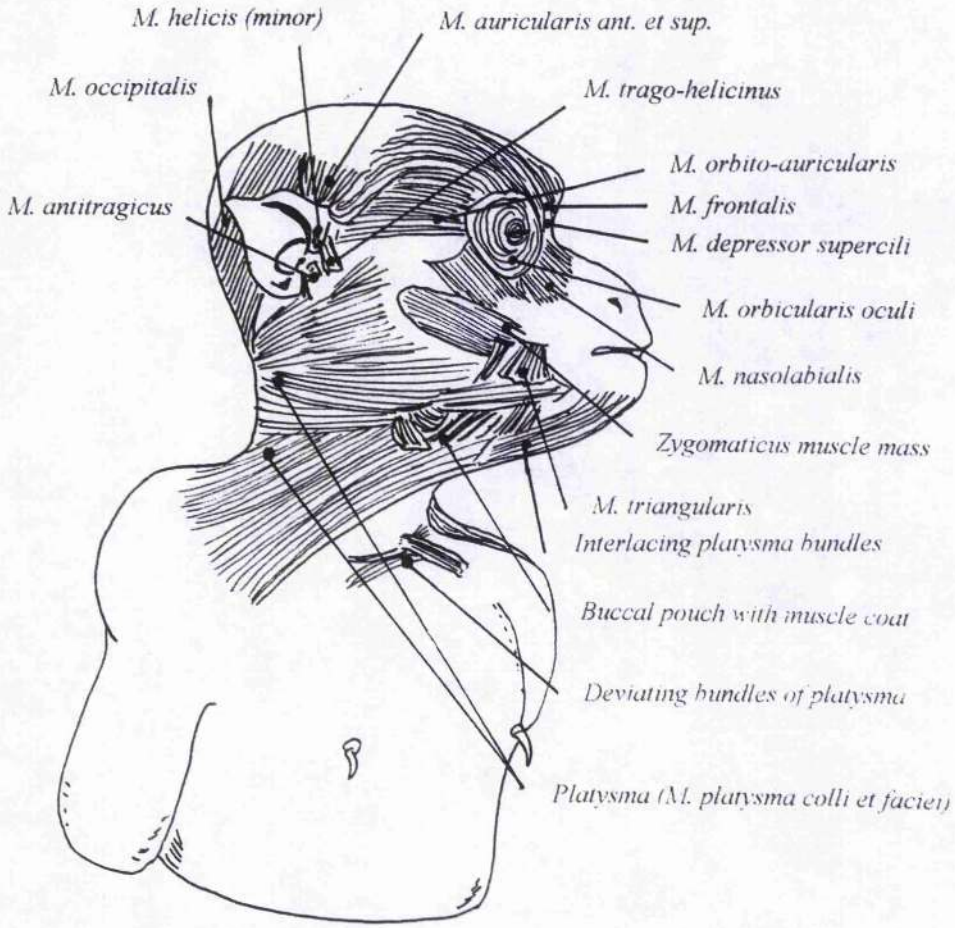
The primate face has also evolved an elaborate system of facial musculature which aids in producing clear facial expressions (Huber 1939, 1961, see Figure 2.2). For example, in the rhesus monkey, the muscles surrounding the eyes (*Muscularis orbicularis oculi*) enable the gross movement of the eyes and with the *M. frontalis* (the muscle controlling the eyebrow ridge), the monkey can produce threatening stares. The *Zygomaticus* muscle mass and the *M. triangularis* provide the jaw with the manoeuvrability to masticate, but would also function in lip-smacking and teeth chattering (Huber 1931). The *M. obliqui et transversi* and the *M. Auricularis* posterior connected to the back of the ears, may also function in threat sequences and submissive behaviour.

Other parts of the body, such as tails and extremities are important tools in social communication (Hinde and Rowell 1961, Bertrand 1969, Sade 1973). Non-ape species may use the orientation of another's body to decipher where they are attending. Apes would also have to use such cues if a second individual's head and eyes were occluded from view, too small to distinguish with any degree of accuracy, or hidden in shade or darkness. It would appear to be relatively easy to determine the direction in which a body is pointed if a quadrupedal stance is adopted. Humans rarely adopt this posture, remaining in a more upright bipedal stance. Monkeys and apes may not require a better means of inferring attention direction than head direction or body posture. Body orientation, head direction and eye gaze direction are in congruent directions for the majority of time spent foraging, grooming, eating, playing and fighting.

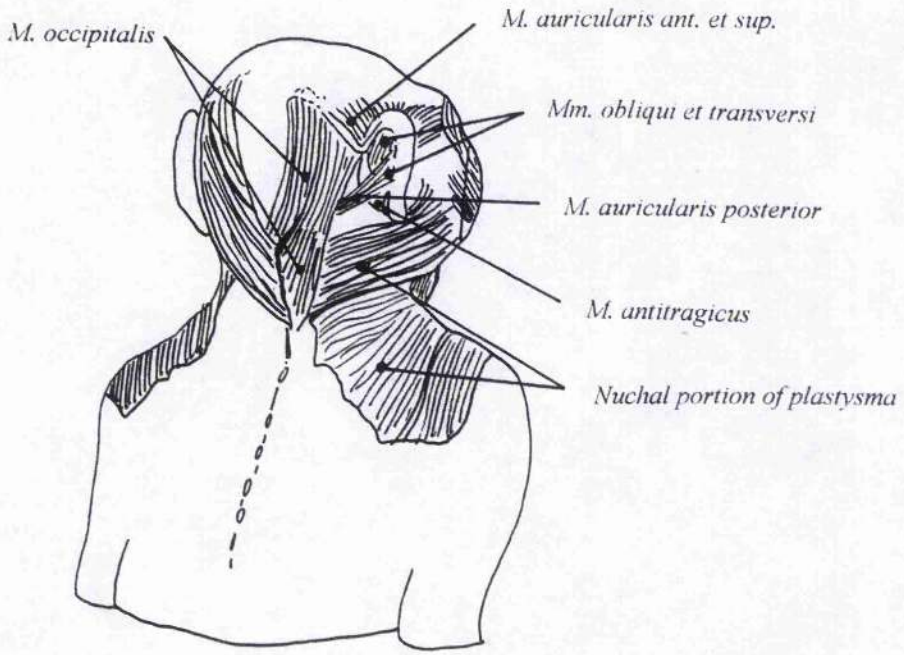
Body size would also appear to be a constraint on what information is gained from the eyes, head and body. Bigger eyes (or head, or body) are easier to see, and therefore easier to gain information from. It would seem reasonable to suggest from other allometric measures that as body size increases, so does the size of the head. This is, however, not necessarily true for eye size. Solitary prosimian species without a substantial need for social communication via the visual channel, have small bodies and heads, but very large eyes (relative to the size of the face). Although an anatomical

Figure 2.2. Drawings displaying the superficial facial musculature of the rhesus macaque (*Macaca mulatta*); **(a)** lateral, **(b)** posterior and **(c)** fronto-lateral views. Adapted from Huber (1961).

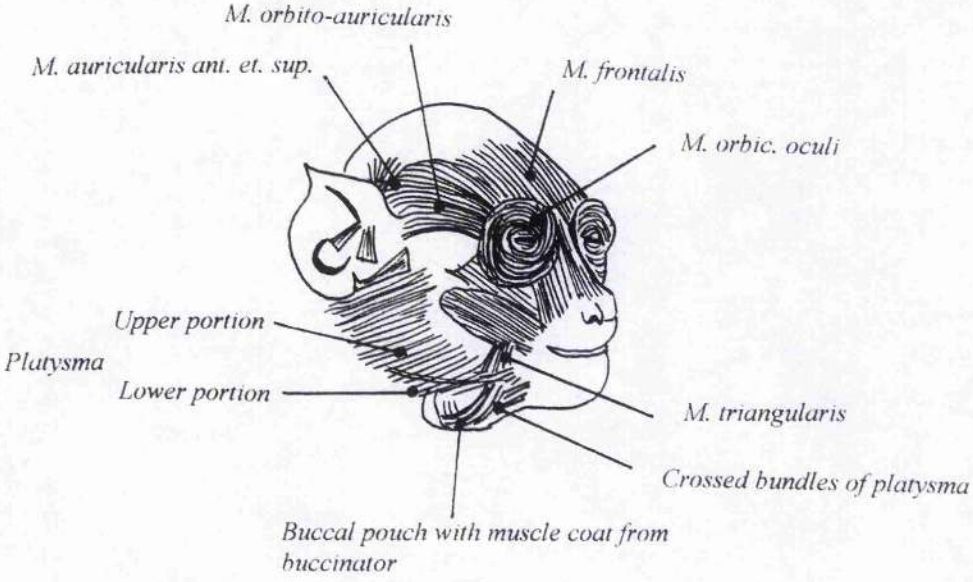
(a)



(b)


M. occipitalis
M. auricularis ant. et sup.
Mm. obliqui et transversi
M. auricularis posterior
M. antitragicus
Nuchal portion of plastysma

(c)


M. orbito-auricularis
M. auricularis ant. et. sup.
M. frontalis
M. orbic. oculi
Upper portion
Platysma
Lower portion
M. triangularis
Crossed bundles of platysma
Buccal pouch with muscle coat from buccinator

change may be beneficial or detrimental to a particular behaviour, this does not mean that the presence of such a morphological change is in a causal relationship with that behaviour. For example, the increased size of the eyes in prosimians are attributable to a nocturnal use of vision, but would also be advantageous to those primates using complex forms of visual communication in a different environment (diurnal primates).

The change in face and body anatomy has not been paralleled by the eyes. Although size differences are plainly apparent, the actual morphology of the eyes themselves does not appear to differ between the many species of primate. The most obvious contrast between species is the relationship between the dark iris/pupil and the white or light brown sclera. A high level of dark iris compared to sclera has been reported for the majority of primate species (Kobayashi and Kohshima 1997). The major extent of the visible eye is taken up by the dark iris and a very small part by the white sclera. Humans, in contrast have a large extent of white sclera, either side of the dark central iris (when looking forward). This ratio may be one of the factors which has allowed humans to use the orientation of other's eyes for learning about objects in the environment (referential communication), whereas non-human primates may be less reliant on such cues (see later discussions).

The morphology of the body, face and eyes provide a set of constraints for primates' use of gaze in a communicative capacity. Another set of constraints are provided by the ecology of the environment in which the primates survive. The transition from an arboreal (tree-living) to a terrestrial (ground-dwelling) environment caused a dramatic change in the sensory emphasis of communication. Tree-dwelling prosimians and New World monkeys mainly use two forms of social communication; audition (vocalisations) and olfaction. A forest environment is very dark, not just at night, but also as the large overhanging branches cause almost total darkness during the day. Both of these forms of communication have two distinct disadvantages from visual communication. They are indirectly focused (anyone within range can hear a call, or smell an odour, including predators), and would seem to be limited to communicating about emotional state ("I'm ready to mate") or spatial position ("I'm over here"), and less

appropriate for communicating information about objects in the environment (unless used in conjunction with visual communication, "Look at that fruit tree").

The move from an arboreal to a terrestrial environment also caused a massive change in lifestyle; nocturnal to diurnal. Visual communication is basically impossible at night and is curtailed during the day, in the dark of the forest. Although a nocturnal existence does have some distinct advantages over a diurnal one (predator avoidance, ease of catching sleeping prey, food abundance, etc., van Schaik and van Hooff 1983), the reduction or complete absence of visual social signals halts other (perhaps better) forms of social communication from developing. This would restrict the amount of information which individuals could communicate, and this would have the knock on effect of limiting social group size (van Schaik 1983).

2.1.3 Primate social structure

Animals cannot live a wholly solitary existence. They must interact with at least one other member of their species to procreate. Sex is the most obvious and important expression of social behaviour. Interaction between animals, however, does not have to be for social or sexual reasons; for example, as a rabbit fleeing a fox, or a lion stalking a zebra.

Social interactions keep a group together and relatively stable. Effective social communication aids in successful social interactions, and therefore assists in maintaining group stability. A minor digression; why does a group form the size it does? Many theories have been proposed as to why group life is beneficial (in an evolutionary sense) compared to a solitary existence (Jolly 1972, Smuts et al 1987). Territoriality, intrasexual competition, predator pressure, food density and food distribution are some of the suggested reasons (van Schaik and van Hoof 1983). Beneficial may be the wrong term, as other less social species survive (and have survived and adapted) for millions of years, and do so to this day. Larger groups may have been beneficial to a certain species during

a particular 'Environment of Evolutionary Adaptation' (EEA), i.e. during a particular evolutionary time and in a particular environmental niche (Tooby and Cosmides 1992).

Primates are one of the most diverse collection of species in the animal kingdom. They inhabit a wide variety of ecological niches, from the jungles of east and west Africa, the rainforests of Borneo, South America and Asia and the snow-topped mountains of Japan (Jolly 1972, Smuts et al 1987). Although the primates are considered successful due to their abundance, a large number of species are close to the verge of extinction (such as the mountain gorillas, bonobos, orangutans, lion-tailed macaques, langurs and ring-tailed lemurs).

Primates differ, not only in their location, habitat and anatomy, but also in their social structure and methods with which they maintain this structure. Rhesus macaques live in relatively large social groups with sizes ranging from 9 to 80, with few males and large ratio of females with infants, and a collection of mixed sex juveniles (Melnick and Peral 1987). Males tend to leave the group once they have reached sexual maturity, so they will have a greater chance of breeding success without competition. The males are hierarchically organised depending on their age, size, fighting ability and length of time in the group (de Waal 1987; Wrangham 1987). The dominant male has the choice of the breeding females and this pre-determines the hierarchical status of the females. Infants and juveniles are organised by their mother's social status.

The social group remains stable by a variety of methods. Affiliative behaviours such as grooming, co-operation and aggressive behaviours keep the hierarchy of the social group stable. Reconciliation behaviour may help group stability, as alliances are formed and after fighting, protagonists spend substantial efforts to "make-up" (Walters and Seyfarth 1987, de Waal 1989). (It is noted that rhesus macaques are not as conciliatory as other primate species studied, such as stumptailed macaques, chimpanzees and bonobos; de Waal 1989.) The majority of grooming occurs between kin, especially between mothers and their infants. Dominant females tend to be groomed by subordinate females and females also groom the dominant male. The dominant male can also be groomed by less dominant males, mainly as a gesture of appeasement. Appeasement may also take the form of mounting; the lesser dominant male, will allow himself to be

mounted by the dominant male to diffuse aggressive situations. The social group has been defined as having "a high level of communication between its members, with a steep falling off between members and non-members" (Jolly 1985).

2.1.4 Social perception

Are faces special for primates? This may seem an obvious question at first glance; of course faces are special. Are we, however, answering this question from an anthropomorphic viewpoint? We know that faces are special for humans; they convey information about emotional states which in turn guide the behaviour of others. Do non-human primates use information from the face in the same or similar ways as humans? The goal of this section is to review and evaluate the experimental and behavioural evidence that non-human primates process faces in similar ways to humans, and that neuroscientific studies of monkey face processing may be useful models of the neural mechanisms of human face recognition (see also Section 2.2.3).

Faces provide large amounts of information about an individual's species, sex, identity, age, health, emotional state and who and what they are directing their attention to. Studies of laboratory primates have provided a wealth of information about how primates perceive faces. How primates respond to faces in their natural environment will be treated later in this section.

Primate faces are a distinct class of objects, with a basic uniform structure (two forward eyes located near to the top of the face, a nose underneath, a mouth underneath the nose and two ears on either side of the face at the external barrier of the face). As faces are so uniform in their structure, and because they are so important in social communication and identification, they have been the subject of psychological studies in human and non-human primates for a number of years. A wealth of information exists in the realm of human face processing; it is reviewed in a number of sources (Bruce and

Young 1986, Bruce and Green 1990, Johnson and Morton 1991, see also papers in Bruce et al 1992).

Monkeys can discriminate faces of other monkeys very easily and manipulations of colour, orientation, size, illumination and posture do not effect these responses (Rosenfeld and Van Hoesen 1979). Vocalisations and corresponding facial expressions were associated with the presentation of the novel faces, suggesting that the monkeys were classing the faces *as* faces, not random objects. There is some disagreement concerning monkeys ability to recognise inverted faces. In the human literature, humans discriminate inverted faces slower than upright faces (Yin 1969, Valentine and Bruce 1986). The same inversion effect has been replicated for squirrel monkeys viewing human faces, but not for squirrel monkeys viewing squirrel monkey faces (Phelps and Roberts 1994) The face inversion effect has also been replicated for rhesus monkeys, where there is an inversion effect for rhesus monkeys viewing human faces, but not for rhesus monkeys viewing rhesus monkey faces (Wright and Roberts 1996). This difference between species faces has been partially attributed to monkey behaviour. Rhesus and squirrel monkeys spend large amounts of time in the canopy of trees, upside-down. Humans, in comparison rarely spend time in this position, so the mechanisms requiring a quick analysis of inverted faces would not have been adapted for. Chimpanzees do not spend large amounts of time upside-down and Tomonga, Itakura and Matsuzawa (1993) found that an inversion effect similar (but to a lesser degree) to the human face inversion effect was present in a chimpanzee viewing chimpanzee and human faces.

Monkeys also prefer faces to either have all component parts of the face present or all component parts to be in the correct configuration (eyes at the top, mouth at the bottom, etc.). Keating and Keating (1982) studied the eye movement responses of rhesus macaques viewing schematic faces, where the component parts were jumbled. They found that monkey subjects looked less at jumbled faces, and less at the eye region when the eyes were in inappropriate positions. Keating and Keating (1982) had previously found that rhesus monkeys spent longer looking at the eye region than any other part of the face (see also Chapter IX). Mistlin (1988) tested stumptailed macaques' emotional reactions to 3-D faces with scrambled features. More appeasement gestures (teeth-

chattering) were elicited when viewing faces with normal configurations of features than jumbled features, suggesting that the subjects could discriminate between faces on the position of the internal components of the face. This effect was lost when the superior temporal sulcus was removed (Mistlin 1988). The eyes were also important when rhesus monkeys viewed photo-fit pictures of human faces. Keating and Keating (1993) again measured eye movement responses to rhesus monkeys viewing pictures of humans. The individual parts of the face could easily be removed or rearranged. They found that the eye region gained the highest amount of attention, but that when this region was removed (or other single parts of the face) face recognition was not disturbed. Only removal or alteration of the eyes and the brows affected face recognition.

The final area where monkeys have been tested is their responsiveness to differing facial expressions. Primates use a wide variety of facial expressions in a number of different contexts (see van Hoof 1962, Andrew 1963a, b, Bolwig 1964, Redican 1975 for reviews). The main expressions used across all primate species are threat, grimace, yawn and lipsmack. Facial expressions are not just methods for conveying a producer's emotional state, they can also be interpreted as providing clues to another's intentions. For example, a subordinate monkey may attempt to surreptitiously mate with a high-ranking female. The alpha male witnesses this attempted clandestine mating, and subsequently threatens the subordinate animal. The information provided in the dominant's threatening gesture is not just emotional (i.e. "you have attempted to mate out of rank, I am angry"), it may also provide information about the alpha male's intentions ("if you don't appease me, I will attack").

Facial expressions can also be used to transmit information about objects in the environment. For example, Mineka and colleagues studied observationing conditioning of snake fear in laboratory raised rhesus monkeys. The young monkeys were not initially fearful of the snakes, or objects which looked like snakes. After observation of their parent's fearful expressions directed towards the sankes, the young rhesus monkeys became fear conditioned to the presence of snakes and snake-like objects. Interpreting that the fearful expressions were directed towards the snakes and linking fear to the snake would be essential for conditioning.

The ability of rhesus monkeys to use facial expressions to transmit information about imminent outcomes, was studied by Miller (1967, 1974). Two monkeys were first tested individually, then simultaneously in view of each other. First, the monkeys had to make a particular response when one of two stimuli was presented. When stimulus A was presented, the monkey had to pull a handle to avoid a shock, and when stimulus B was presented they had to pull a different handle to gain a food reward. The monkeys were then tested together (in separate primate chairs). One of the monkeys could see the two stimuli, but had no access to the two handles, and the second monkey had access to the handles, but could not see the stimuli, only a video picture of the other monkey. The monkey with access to the handles had to pull the correct one for both animals to receive a food reward and for the second monkey not to receive a shock. The monkey learned to respond to the facial expressions of the second monkey when the monkey was familiar, but responses were poor when the second monkey was unfamiliar to the first.

It therefore appears that rhesus monkeys, at least, are capable of transmitting information about unpleasant experiences to conspecifics, by the use of expressive behaviour (e.g. facial expressions. Can monkeys transmit similar levels of information about unpleasant foods to others? Pig-tailed macaques and spider monkeys were tested in the laboratory and the wild for their ability to warn others about the poor quality of foods they had eaten (Fairbanks 1975). It is ultimately important that information about inedible or toxic foods is transmitted to the whole group to avoid illness, reducing the reproductive capabilities of the group members. No evidence of social learning was found when a pig-tailed monkey *modeller* tried a distasteful food (a drugged fig) in the presence of three *observers*. The observers did not change their eating behaviour in reaction to the modeller's behaviour after eating the food. This result was replicated when a novel food was presented; hesitancy increased, but the observers still tried the novel food. Free-ranging spider monkeys would try novel foods (bread coloured red, green, yellow or blue), even after observing another individual's reaction to the distasteful foods.

Fletemeyer (1978), however, found that a hierarchy existed within chacma baboon society, which determined which individual tried a novel food first. Whilst

attempting to capture these wild baboons (using drugged oranges), the alpha dominant male would approach the orange, unpeel it and then discard it. Subadults and juveniles would then approach the orange, but be threatened away by the alpha male. The most dominant individual, therefore appeared to determine whether the food was safe, through individual experience and then transmit this information to conspecifics. Fletemeyer (1978) suggested that:

"social communication behaviour manifested in a network of threat-avoidance responses by conspecifics is highly adaptive to a baboon troop because it is a more efficient and safer means of assessing the quality of edible items than is individual experience" (p. 223).

Faces are a special category of objects for laboratory primates, but what is the evidence that faces are just as important for free-ranging monkeys and apes? A certain number of gestures, postures, facial expressions and body movements are associated with primate social behaviour (Hinde and Rowell 1961). Non-human primates engage in at least three types of social behaviour, where they require such special forms of visual communication; agonistic, affiliative and sexual behaviour. In the monkey, the eye region of the face is of particular importance (see Chapter IX for review) for affiliative and threatening behaviours (Redican 1975, Keating and Keating 1982) and sexual behaviours (Linnankoski et al 1993). Eye expressions that comprise agonistic gestures include the stare, apprehensive looking, eye-contact avoidance, feigned indifference, feigned interest, and ignore (Hinde and Rowell 1962, van Hoof 1962, Bertrand 1969). The direct look without the raising of the eyebrows seen in the agonistic stare, is a friendly gesture. Linnankoski et al (1993) found in stump-tailed macaques that direct eye-contact from the female caused sexual arousal in males culminating in masturbation. Facial expressions provide more information about the `internal' states (feelings and intentions) of an individual, than most forms of visual social signal. During agonistic encounters, a monkey employs a large number of facial expressions (van Hoof 1962, 1967, Andrew 1963, Bolwig 1964, Redican 1975). The attack face is displayed when the monkey is ready to attack, usually after the monkey has displayed an open mouth threat face, a pant threat

face or a bared teeth threat face (Bertrand 1969). Each of these faces has a particular meaning in the aggressive act. Appeasing facial expressions include the bared teeth threat face, grin face, teeth chattering face and the lip-smacking face (Bertrand 1969, Maestripieri 1996 a, b). As stated above, facial expressions are also employed in friendly situations, for example, the pout face, play face, laughing face and the kiss. The direct look can not only function in aggressive encounters, but also in affiliation (de Waal 1989). Although this eye expression is similar to the antagonistic stare, it is employed without pushing the ears back or the head pushed forward, as would be seen in aggressive stares. There are many different gestures, postures and motions which are used to display emotional/social states in macaques (Hinde and Rowell 1961). Agonistic gestures include pulling, pinching, grabbing or plucking fur; pushing and kicking, dragging, branch shaking, repeated bouncing and rocking, and submissive gestures include chasing, withdrawing or displacing, moving away, fleeing or crouching and remaining passive (Bertrand 1969). Affiliative gestures and postures are easier to evaluate and include grooming (fur kneading), embrace or arms around another monkey, huddling, sitting in close proximity to another and keeping company.

Sexual gestures form an important part of social behaviour. Problems in interpreting and recognising sexual signals lead to problems in breeding. Sexual signals are often used in conjunction with olfactory cues; this may be to substantiate the message transmitted by the visual cues, so that the correct information gets through to the chosen mating partner. Visual sexual signals include presenting to the prospective sexual partner. Presenting has a multitude of functions, a solicitation to mate, rank recognition, a permission-seeking gesture, an appeasement gesture, an enlisting and excitement gesture, a particular play pattern, a signal for dorsal clinging and a solicitation for grooming (Bertrand 1969). To dissociate the particular intention of the presentation, the present must be given in a particular context, with an individual's history. This is possible via a specific presenting sequence by the mounter, consisting of perineal investigation, hip touching, forced lifting of the mountee's hindquarters, sitting, crouching, or walking away, then looking at the mountee and then possibly harassing the mountee. Other sexual signals in macaques include genital rubbing, penis and labia presenting, genital

manipulation and masturbation (Bertrand 1969, Bolwig 1978). Also in relation to visual sexual signals, monkeys must have sufficient colour vision to react to the deep reddening of the females genital region during oestrous.

Monkeys and other non-human primates use particular locomotor patterns, which can be used and interpreted in a communicative manner. Examples include quadrupedal walking, cantering, carrying gaits, bipedal stance and run, climbing up and down, leaping, swimming, jumping, hanging by arms or legs, running, and sliding (Bertrand 1969). Maternal behaviour also has a variety of expressions, gestures and postures connected with it. Grooming, obviously is a specific part of the maternal process; as are licking and cleaning. Mothers also cradle their infants and the infants cling ventrally to their mothers or climb on top of them.

A wide variety of these various social signals must be interpreted by others in the social group for the survival of the individual members (Zeller 1987, 1992). For example, an infant needs to interpret their own mother's actions to gain food, and to know where they can seek protection. Others must know when they are being threatened or attacked, whether to retaliate, to retreat, or to defend themselves. They must also know the other individuals in the social group and their particular positions in the hierarchy of the group (see Chapter VIII), so as to avoid such conflicts and to possibly solicit help from others (Cheney and Seyfarth 1990c). It would also be beneficial to know and predict the intentions of others in the troop. This may be knowing that another intends to mate, that a threat is only in play, or that a chase is from an aggressor and not in play; so that appropriate actions can be taken. This is discussed below and in Chapters VII and IX.

2.1.5 Social cognition

It is important, not only to perceive the signals of a second party with whom communication is desired, but also to understand the presented signals of the second individual and the context with which the signals are displayed. Whether monkeys and apes understand the signals of others, rather than just reacting to them; is a controversial

area of what has been termed "cognitive ethology" (Griffin 1978, see also papers in Harre and Reynolds 1984 and Ristau 1991).

A useful example of this form of argument is vervet alarm calls and predator avoidance. A number of experiments by Cheney and Seyfarth (reviewed in 1990c, see also Seyfarth, Cheney and Marler 1980a, b) have led to discussions of social cognition, or understanding of the complexities of the social world in monkeys and apes. Cheney and Seyfarth studied the different form of alarm calls that vervet monkeys use when in the presence of predators. These calls have the subsequent action of alerting conspecifics to the presence of different types of predators. Vervet monkeys have three natural predators, eagles, leopards and snakes and each predator is represented by a different alarm call. When a *snake call* is vocalised by a member of the troop, the other monkeys which heard the call look down on the ground to look for a snake. Likewise, if a vervet uses an *eagle call*, the other vervets look into the sky and run into the vegetation. If a vervet spies a leopard and gives a leopard call, other vervets look where the caller is directing their attention and run in the opposite direction.

The question remains, are vervet vocalisations in response to the appearance of predators, emotional reactions to a predator, or are they part of a deliberate altruistic warning system used to refer others to the presence of a predator (voluntary signalling)?. Two issues are raised here. First, for the signaller to use alarm calls as part of a warning system, they must have *intended* to have given the call, and within the vicinity of conspecifics. If this was the case, a lone vervet confronted with a predator would either not call or would not continue its calling. (An emotional call would be short and not continuous.) Cheney and Seyfarth (1985b) tested the alarm responses of vervets in an enclosure to the presence of an unknown human. Usually, a vervet in a group would call in the presence of such an aversive stimulus. When a lone vervet was sectioned and presented with a similar stimulus, it did not call. Cheney and Seyfarth (1990c) also describe an incident where a single vervet was separated from her troop and was being followed by a leopard. When the monkey was chased by the predator, she was totally silent, making no leopard calls. If the call were emotional reactions, the monkey would be

expected to call. (It is possible that the monkey in this instance was too frightened to respond vocally.)

Second, for the call to have meaning to other group members, the vervets must have the ability to understand the nature of the call (and to not just respond to any call given). This would appear to be the case, as an appropriate behavioural response is elicited from the vervet troop, rather than a random response (Seyfarth et al 1980a). A random response would develop from a call with no informational content; a call which was a basic emotional reaction to a stimulus.

To determine that the alarm calls were informational in content, Cheney and Seyfarth (1990c for review) used play-backs of different alarm calls when no predators were present. Initial responding was as predicted; the monkeys acted as predicted to the individual calls, i.e. running into the bushes after hearing the play-back of an eagle call, or looking at the ground after hearing a snake call. The monkeys, however, began to become habituated to the same call of the same individual (who would be "crying wolf"). If the same individual provided a different call, the response was as active as previously described (Cheney and Seyfarth 1982, 1988). This experiment also suggests that the vervets can identify others by their alarm calls (as they could interpret the same alarm call as coming from the same individual).

In discussing whether monkeys understand others signals as intentional or as 'outcrops of their minds', a slight digression is required. Dennett (1987) has proposed a theoretical framework to be used in all discussions of non-human primate mental attribution. Dennett suggested that "the intentional stance" would be a useful framework for interpreting experimental and observational studies of primate social cognition. The intentional stance works on a number of (possibly infinite) levels. Premack and Woodruff (1978) were the first to coin the phrase, theory of mind (mental state attribution, mindreading, folk psychology, etc.; for discussion see Whiten 1994, 1997a, b). The intentional stance is the same as theory of mind; the proposition that others have beliefs, desires, goals and these mental states can be inferred from others behaviour. Evidence for and against a non-human primate theory of mind is evaluated in Chapter VII (see also Povinelli and Eddy 1996c, Whiten 1997a, b, Tomasello and Call 1997).

There are a number of *levels of intentionality* with which an individual can interpret another's mental state (Dennett 1983). The lowest level (*zero-order* intentionality) suggested that Monkey X produces an emotional reaction to a stimulus, such as an alarm call. *First-order* intentionality suggested that Monkey X *wants* to produce the alarm call (as discussed earlier). Higher orders of intentionality are, Monkey X *wants* to produce the alarm call so that Monkey Y *believes* there is a predator present (*second-order* intentionality). *Third-order* intentionality becomes more difficult to interpret; Monkey X *wants* Monkey Y to *believe* that Monkey X *wants* Monkey Y to escape the predator. Dennett suggests that human can interpret up to six-orders of intentionality without getting into great difficulty.

This is a useful method for thinking about social cognition, but is basically weak in that it is almost impossible to prove experimentally. The work of Cheney and Seyfarth and others, have provided monkeys with at least *first* and possibly *second-order* intentionality. The difference between non-human and human primates appears to be the differences between recognition and understanding of a) behaviour and b) mental states. This difference is discussed further in Chapter IX.

Social cognition requires not only the ability to understand others' behaviour (and mental state), but probably more importantly, their social position. As has been discussed earlier, monkey and ape groups are organised hierarchically; the most dominant male has the most access to females for breeding, and is usually the most aggressive or most able to form coalitions (de Waal 1982, Byrne and Whiten 1988). The females are also hierarchically organised, due to physical attributes, access to the alpha males and ability to form coalitions with others (males and females). Monkeys are particularly apt at recognising others' social relationships (Cheney and Seyfarth 1990b). Dasser (1988) reports an experiment where long-tailed macaques discriminated mother-infant pairs from other female-infant pairs (for full discussion of this experiment see Chapter VIII).

Monkeys and apes have the ability to recognise others dominance (or subordination) from cues such as physical strength, amount of grooming received and given, access to mates, access to food and the attention afforded by other group members (Chance 1967). For example, Monkey X receives the largest amount of attention from

other group members, is large and copulates the most. It can therefore by reasonably inferred that this animal was the most dominant in this particular troop. Monkey and apes must have adapted to make this inference, as inappropriate action against a more dominant animal could be fatal. This appears to be the case (Cheney and Seyfarth 1990b, c).

The ideas presented in this section are basic to the rest of this thesis. Monkeys (and apes) can recognise others social relationships, kin and individuals and recognise their social signals. The next section discusses how the monkey brain may achieve this level of recognition.

2.2 Neurobiology of Primate Social Behaviour

2.2.1 Criteria for the inclusion of area X as part of the "Social Brain"

Before discussing the evidence for and against the inclusion of certain brain regions as belonging to the "social brain", a number of criteria need to be fulfilled. The following list is not exhaustive, but is a useful guide to the warrants of inclusion. At least one or more of the following is required for inclusion.

1. Lesions to area X or ablating the primary input source to area X disrupts normal social behaviour (see below).
2. A number of cells in area X respond to social stimuli, or to stimuli which can be interpreted as functioning in social behaviour or cognition, decision-making and social memory or whose output produces some aspects of social behaviour (see Chapters VII & VIII).
3. (a) Profuse anatomical connections of area X and other regions which function in social behaviour (see Chapter V). (b) At least one of the inter-connected areas should extensively connect with appropriate input and output structures, which code sensory,

motor and regulatory processes (such as visual, auditory, somatosensory and motor cortices, hypothalamus and brainstem, see Chapter IV)

4. Area X has an evolutionary adaptation for social behaviour coding, i.e. area X codes for social behaviour in a sample of species with a distinct evolutionary history. Neuropsychological studies suggest that the human brain uses the same areas as the monkey brain for coding social behaviour. The evolutionary history can be further tested using comparative anatomical and ecological analyses (see Chapter VI).

5. Pharmacological agents known to cause changes in social behaviour, act on area X (amongst others, see section 2.2.4).

6. The social behaviours which are related to the function of Area X are definable within the context of the typical responses shown by all animals in the species. Using a hypothetical example; if all members of a species have the same lesion of area X and all the individuals have identical attributes (e.g. age, sex, social status, medical condition, etc.), then the same effects on social behaviour would be seen throughout the group. This proposition is unfortunately very difficult to test empirically.

Three regions of the macaque brain will be discussed using the above criteria to determine whether the evidence suggests their involvement in coding aspects of social behaviour. The following literature review will put the area into context by discussing the neuropsychological (criterion 1) and neurophysiological (criterion 2) evidence for their inclusion. The third section will discuss a possible evolutionary continuity between monkeys and humans by discussing lesion effects on social behaviour in human patients (and neuroimaging data on normal human subjects).

Criterion 3(a) will be discussed in Chapter IV where the connections of these three brain regions are analysed using a new statistical method called non-metric multidimensional scaling (NMDS). Criterion 3 (b) is discussed in Chapter III and the evolutionary stability of the previous proposal (criterion 4) is tested in Chapter V using comparative and ecological data for a range of non-human primates.

Criterion 2 is further tested using neurophysiological methods (described in Chapter VI) by testing whether single cells in one of these regions (anterior temporal cortex) respond to a range of stimuli which aid in social recognition, interaction and

cognition. Chapter VII evaluates a complex level of processing, i.e. where others are attending, moving and what they are interacting with. Social interaction is improbable when another's attention is directed elsewhere. Chapter VIII looks at neurons which may contribute to signalling which species individuals are interacting with; a primary level of social interaction. Such levels of visual processing may contribute to the perception of another's intentions and plans as suggested by a theory of mind (see Chapter IX).

2.2.2 Lesions of the Social Brain

As can be seen from the examples above, monkeys, apes and humans use a variety of complex methods to facilitate interactions with members of their social group. How is this information recognised and processed in the primate brain? Brothers (1997) has stated that the brain is an organ designed for processing such social interactions. This idea is certainly not a new one; this section aims to review and evaluate the last 100 years of research in this area and to provide a theoretical framework for some of the empirical work in the rest of this thesis.

Brown and Shafer (1888) performed the first study to find a correlation between brain lesion and a profound loss of social function. Ablation of the junction between the temporal and the occipital lobes in the rhesus monkey brain caused substantial disturbances in visual and emotional behaviour. These findings were replicated, substantiated and expanded in the 1930's by Kluver and Bucy, who lesioned the anterior temporal cortex (Kluver and Bucy 1937, 1938, 1939). The lesion they produced was quite large and included the hippocampus, uncus, amygdala, tail of the caudate nucleus and most of the anterior temporal cortex (including the inferotemporal cortex, entorhinal cortex, parahippocampal gyrus, rhinal cortex and superior temporal cortex (Kluver and Bucy 1939). This lesion caused a marked and distinct behavioural and emotional change post-operatively, in a number of monkeys, each with well defined symptoms. In what has now been termed the Kluver-Bucy syndrome (KB-syndrome), the monkeys developed symptoms of *psychic blindness* (or the tendency to approach animate and inanimate

objects without hesitation); excessive oral tendencies (the monkeys examined all objects, foods and non-foods by mouth rather than hand, with all the objects being examined again and again as if novel); *hypermetamorphosis* (or the tendency for the monkey to attend and react to every visual stimulus); visual agnosia (a disturbance in general object recognition); emotional changes (such as the complete absence of fear and anger); and hypersexuality (such as excessive masturbation, copulation and fellatio, either when alone or in the presence of other monkeys). It is impossible to say that these deficits were purely due to effects of social behaviour as the subjects were all housed singly. It is also difficult to say exactly which brain regions were involved in which deficits as such a large area of cortex and subcortex was removed. These issues have been addressed in more recent experiments.

The symptoms of the KB-syndrome have been replicated in a series of experiments by Horel and colleagues (Horel and Keating 1969, 1972; Horel and Misantone 1974; Horel, Keating and Misantone 1975). The lesions made during these studies were restricted to either the bilateral whole temporal lobes; the unilateral temporal lobe, contralateral occipital lobe and sectioning the corpus callosum; the amygdaloid complex, or transecting the visual inputs to the temporal lobe from the visual cortex. These different lesioned animals were then compared for their abilities in tasks designed to test for components of the KB-syndrome. They discovered that partial symptoms of the KB-syndrome could be fractionated by combinations of these lesions. By ablating the middle and inferior temporal gyrus (inferotemporal cortex), the visual deficits seen in the KB-syndrome could be clearly differentiated. The visual tests used were a visual pattern discrimination task, and a food/non food discrimination. The temporal cortex lesioned group were found to be severely impaired in the pattern discrimination test, but not in the food/non food test. By ablating the amygdala, the emotional deficits seen in the KB-syndrome were plainly apparent (for example, decreases in attack, escape and submissive behaviours, but no change or slight increases in approach behaviour; Horel and Keating 1975). Hypoemotionality was only present after amygdala only lesions, suggesting that the amygdala was the next logical stage in processing visual information which was then granted emotional value. The temporal

cortex lesioned group did not show any emotional disturbances, but only displayed disturbances of complex pattern recognition.

This interpretation would appear to be correct from the anatomical connections of both of these regions (see Chapters III and IV) and the properties of neurons in these two regions. Horel and Keating (1972) also determined that it was the visual input to the amygdala which was causing deficits in the KB-syndrome, in particular the emotional deficits. They determined this by lesioning the temporal lobe on one side, lesioning the contralateral occipital cortex and disconnecting all possible visual inputs to the amygdala, such as transecting the circumstriate cortical belt, lesioning the anterior commissure, lesioning the contralateral temporal lobe and cutting the corpus callosal connections between the temporal lobes. They again tested lesioned monkeys on a two-choice task of non-food versus food; a ten choice task of ten food objects versus ten non-food objects, and emotional responsiveness tests (including assessment of tactile and oral reactivity). After the bilateral total temporal lobectomy, the monkeys displayed the symptoms of hypoemotionality, orality and psychic blindness. The visual deficits seen in the bilateral temporal cortex ablation animals were the same as in the unilateral, disconnection animals (i.e. there was no difference between ablating the temporal cortex from eliminating all visual input into the temporal cortex). Responses to emotional stimuli by the unilateral temporal lobe lesion group were different to the disconnection animals. These animals displayed a deficit in emotional behaviour, but this deficit recovered dramatically over time (Horel and Keating 1972, Horel and Misantone 1974). The authors suggested that this recovery was not due to re-routing of visual information through the intact callosum or into the intact temporal lobe (see also Horel and Keating 1969), but may have occurred through learning, as the recovery was only specific to post-operatively presented objects.

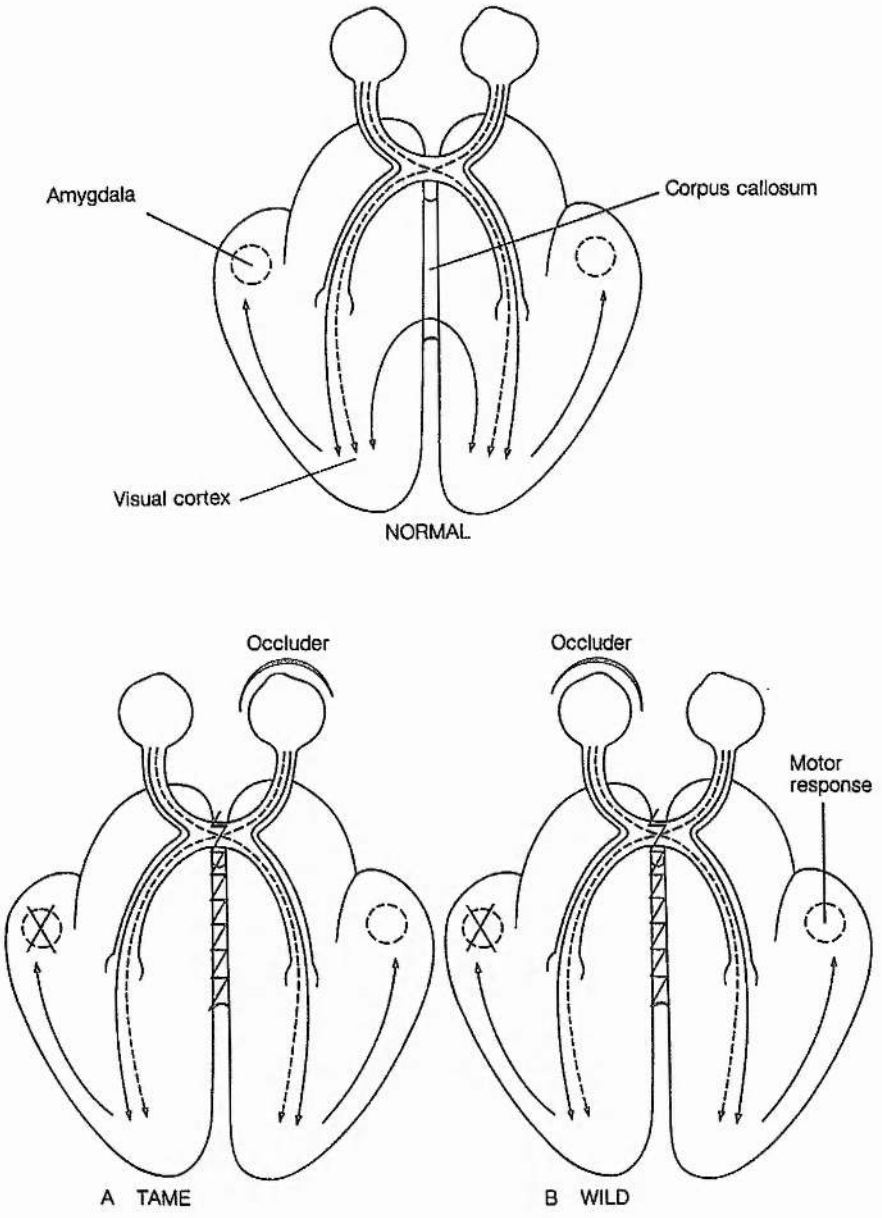
Downer (1961) was the first to suggest that it was the visual information processing in the amygdala which contributed greatly to the emotional and social deficits of the KB-syndrome. In *split-brain* monkeys, with the optic chiasm, anterior commissure and the corpus callosum cut, Downer lesioned the temporal pole, containing the amygdala, and sutured the eye on the contralateral side to the lesion. This caused some

symptoms of the KB-syndrome (visual agnosia and hypoemotionality). Downer then opened the sutured eye and sutured the ipsilateral eye to the lesion. This completely obliterated the symptoms of the KB-syndrome and restored pre-operative levels of visual discrimination and aggression. Downer then proposed that it was the amygdala which was receiving visual information (the deficits in aggression were only seen with visually presented stimuli, not in reaction to vocalisations). A unilateral amygdalectomy was then performed on a monkey with a transection of the optic tract, anterior commissure and corpus callosum, thereby preventing the passage of visual information across the hemispheres. The eye contralateral to the amygdalectomy was sutured, and the animal became placid, as no visual information was reaching the intact amygdala. The eye was then opened, and the animal became aggressive again, as visual information was not able to making its way to the amygdala. The eye on the ipsilateral side of the amygdalectomy was sutured and the animal remained aggressive (as visual information was going to the intact amygdala). Finally, the contralateral eye to the lesion was then sutured and the ipsilateral eye opened and the animal again became placid. (Downer 1961). For a diagrammatic representation of the above experiments, see Figure 2.3.

These results and those of Horel et al. suggested that the major deficits of the KB-syndrome were dependent wholly on bilateral lesions to the amygdala, or eliminating visual inputs to the amygdala and that the original findings of Kluver and Bucy may have been only due to amygdala ablations. In all the above studies, the behavioural reactions of the lesioned subjects were directed to human observers in a non-social setting, and studies concentrated on collecting data on emotional reactions rather than complex social information processing (effects of amygdala lesions on this level of processing will be described later).

Weiskrantz (1956) found that lesioning the amygdala and re-secting the temporal pole of rhesus monkeys caused a reduction in motor activity (the subjects became physically sluggish), approached all presented items (e.g. sticks, gloves, human observers; all previously aversive stimuli) and were generally tame and unexcitable. Again, these are some of the symptoms of the KB-syndrome. Walker, Thomson and McQueen (1953) also replicated the symptoms of the KB-syndrome of apathetic attitude, no apprehension

Figure 2.3. Schematic representations of the various experiments performed by Downer (1961) to study the effects of unilateral amygdala lesions, commissurectomy and eye sutures on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). In the NORMAL condition, visual information reaches the amygdala via the visual cortex on the ipsilateral and contralateral sides. If the amygdala is lesioned unilaterally, the commissure is lesioned, and the eye is sutured on the contralateral side to the amygdala lesion; visual information can not reach the intact amygdala. The animal does not react aggressively to threat stimuli, and becomes TAME. If the amygdala is lesioned, the commissure is lesioned and the eye on the ipsilateral side to the amygdala lesion is sutured; the visual information reaches the intact amygdala. The animal acts appropriately to threat stimuli by being WILD.



of previously feared objects and a reduction in aggression, by ablating the medial temporal lobe (including the amygdala and the cortex surrounding it, such as the uncus, the rhinal cortex and superior temporal sulcus). There was also an increase in signs of affection and affiliation, such as grooming, and licking other monkeys. One interesting example of the reverse of this was seen with a mother and her "perverted maternal instinct" (Walker et al 1953) towards her infant, which included indifference, biting and slapping and rebuffing.

Other deficiencies are observed after amygdala ablation, some of which are part of the KB-syndrome, but not immediately explainable in terms of deficits in emotion processing. Schwartzbaum et al (1961) showed that a bilateral amygdalectomy caused a dramatic increase in locomotor activity , which they described as a "disturbance in the habituation of motor activity". Amygdalectomised monkeys also do not form discrimination-reversal learning sets (which normal laboratory monkeys do), and this may be due to a change in the responsiveness of the monkey to novel items which has been discussed by others (Barrett 1969, Schwartzbaum 1965, Schwartzbaum and Poulos 1965, Gaffan and Harrison 1987, Gaffan et al 1988, Gaffan and Murray 1990, Sarter and Markowitsch 1985).

More recently, Aggleton and Passingham (1981), have tried to replicate the symptoms seen in the KB-syndrome, but by performing subtotal lesions of the amygdala to further fractionate the KB-syndrome into precise anatomical locations within the amygdala. The separate lesions removed either the basolateral complex (BLA), the lateral nucleus (LAT), the dorsal amygdala (DAM) or corticomedial complex, and the whole amygdala (AMX, controls). The monkeys were tested on a variety of formal tests, e.g. food choice from two presented foods, hypermetamorphosis (a free choice of a variety of edible and inedible items), emotional responsiveness to frightening stimuli (such as snakes or the experimenter), and approach behaviour towards a food reward next to an aversive stimulus (an experimenter). All animals with subtotal lesions did not eat (but did touch) meat or faeces, did not show abnormal choices between edible and inedible objects, and did not mouth inedible objects. Changes in levels of emotionality were slight. BLA lesioned animals displayed high levels of aversive/submissive behaviour, one DAM

lesioned animal displayed hypoemotionality, whereas a second DAM lesioned animal showed increased aggression. Monkeys with subtotal lesions tended to use more submissive gestures overall, such as lipsmacking. These animals also showed increased tendencies to approach previously fearedl objects such as human observers. In contrast, animals with total amygdala lesions showed all the signs of the KB-syndrome, they ate meat frequently, showed signs of coprophagia, had an excessive exploratory behaviour (handled and mouthed more inedible objects before edible foods), displayed a remarkable fall in emotionality, and showed an increase in approach behaviours and submissive gesturing (also seen with subtotal lesions).

There are a number of possible explanations for these results. Sensory information reaches the amygdala via the basolateral complex (visual information to the lateral and lateral basal nuclei, auditory and somatosensory information to the accessory basal nucleus). Lesions of cells within these areas should eliminate this information from reaching the rest of the amygdala. In contrast, these subtotal lesions appeared to have little effect on producing the symptoms of the KB-syndrome seen after total amygdala lesions. Aggleton and Passingham (1981) used radio-frequency lesions to destroy amygdala tissue. This method destroys fibres of passage through the amygdala which are important routes by which sensory information may travel to other areas of the brain (such as temporal pole and orbitofrontal cortex) and cell bodies. Ibotenic acid lesions would be required for lesions of cell bodies, without damage to fibres (Amaral, personal communication). It is therefore possible that some fibres were damaged after subtotal lesions and that the deficits seen were a direct consequence of fibre damage, not amygdala damage. . The subtotal lesions may not have removed all tissue within an amygdala division and this remaining tissue may also have been sufficient to perform certain functions.

The next section discusses the evidence that the amygdala is involved not only in basic emotional processing, but is also essential for normal social functioning in dyadic, triadic and larger groups of social monkeys. Rosvold et al (1954) lesioned the amygdala in monkeys to determine the effect on social behaviour, particularly social interaction and dominance hierarchy. The hierarchies of the social groups were determined from a peanut

feeding situation, where a peanut was either offered to one individual or placed between two individuals. The dominance was determined from the frequency of individuals gaining food. This method for establishing dominance relationships has been questioned (Bernstein 1981) and is unorthodox when compared to other methods, such as noting bouts of aggression or fearfulness between different parties (Martin and Bateson 1993). The dominant individual was then given a bilateral amygdalectomy. The animals were also examined in individual cages for their aggressiveness or fearlessness behaviour, threatening and fight behaviour and pellet taking behaviour. The dominance hierarchy of the group before surgery was Dave > Zeke > Riva > Herby > Benny > Arnie > Shorty > Larry. Dave, the dominant male had a bilateral amygdalectomy and became submissive to all, but the least dominant animal (Larry). He did not try to retrieve food and did not react aggressively to, or retaliate against animals who attacked him. The second monkey in the hierarchy, Zeke, then became the most dominant male. Zeke then received a bilateral amygdalectomy and became subordinate to all, but Dave and Larry. This allowed the next dominant animal, Riva, to become the dominant monkey. Throughout all the social encounters, Riva was an aggressive animal, and when he received a bilateral amygdalectomy he remained aggressive. This situation has been explained by the fact that in all the previous social hierarchies, the next dominant animals after the most dominant animal had been aggressive. The next dominant animal after Riva, Herby, however was placid and unassertive, so Riva had no direct competition from appropriately placed males, and therefore remained aggressive. When looking at the effects of brain lesions on social behaviour, it became important to study individual interactions and the personalities of the group members before surgery.

Plotnik (1968) studied the effects of anterior temporal lobotomies (mainly just the amygdala, but in one instance the amygdala and some of the inferior orbitofrontal cortex) on squirrel monkey social dominance ranks and aggressiveness. Plotnik attempted to replicate the results of Rosvold et al (1954) by determining whether individual personalities would determine the dominance hierarchies after each individual's surgery, using a competitive scenario. Plotnik found, however that the stability of the dominance hierarchy after surgery depended on individual animals. White who was dominant before

surgery, still remained dominant, but less aggressive. The next dominant monkey, Green, became more aggressive towards the next monkey in the hierarchy, Red. Similar patterns of increases in aggression emerged for every subsequent monkey after they received an amygdala lesion. All monkeys became tamer towards humans, approached and sniffed all objects and produced less fear of previously avoided objects (as would be suggested by the KB-syndrome).

The proposition that the amygdala is the seat of social behaviour in non-human primates has received attention from a number of experimenters. All the previously described studies of amygdala lesions have been performed in the laboratory on animals born in captivity. As with most investigations into brain-behaviour relationships there are costs and benefits related to where the experiments are carried out. Laboratory experiments afford high levels of control over large numbers of possible variables, but lack the richness of natural behaviour. Experiments in the wild in contrast have low levels of experimental control, but the results derived are closely related to the natural behaviour of the observed animals (in the wild there are many situations which cannot be controlled during the life-history of an animal). Both methods have something to offer this field of research.

Kling has been the major proponent for investigations of amygdalectomised monkeys in their natural habitat (or reconstructions of their habitat). Dicks, Myers and Kling (1969) studied rhesus monkeys in a semi-natural setting (the rhesus monkey colony of Cayo Santiago, Caribbean Regional Primate Centre). They trapped 7 males from a large group of 85 and performed bilateral amygdalectomies on these monkeys. The subjects were then released back to their social group and observed. The lesioned monkeys became solitary and indifferent to the other members of the group and did not appear to respond correctly when attacked (which was frequently). As a number of these operates died alone, location unknown, it was not known whether the lesions affected the whole of the amygdala, part of the amygdala or another part of the brain altogether.

Experimenters have also attempted to study the effects of amygdala lesions on free-ranging monkeys. Kling, Lancaster and Benitone (1970) studied a group of free-ranging vervet monkeys in Zambia, and asked the question "would amygdalectomised

animals survive in their natural environment, and would previous social interactions be re-established?" (Kling et al 1970). Amygdalectomy in the caged vervet caused anorexia, hyperorality, coprophagia and a reduction in fear of humans; all symptoms of the KB-syndrome (Kling and Carpenter 1968). They found that amygdala lesions in free-ranging vervets did not cause characteristics of the KB- syndrome; instead the monkeys did not eat or drink after lesions and no oral behaviour was observed. Post-operatively, the vervets displayed a lack of responsiveness to other group members and did not exhibit any threatening or aggressive gestures to approaching monkeys. Although the monkeys were mainly given friendly and affiliative gestures from other monkeys, they withdrew from their social group and showed a negative response to social interactions. This may be related to ideas that the amygdala places salience on incoming sensory information that allows an animal to respond appropriately to intended social communication. An animal may respond in a threatening manner to every gesture directed towards it and so would fail to facilitate and maintain social interactions and bonding. It would also seem clear that the KB-syndrome (in vervet and rhesus monkeys) is dependent on a solitary existence, as it's effects are diminished within the social context.

Stump-tailed macaques (*Macaca speciosa*) appear to be docile and passive, compared to the aggressive rhesus macaques (Bertrand 1969, Orbach and Kling 1964). Kling and Cornell (1971) suggested that it may be species-specific behaviours which are compromised by lesioning the amygdala, giving rise to reductions in aggression, in the naturally aggressive rhesus macaque. Predictions about the stump-tailed macaque were difficult to make as at the time of this study, the species was little studied, and their passivity was thought due to "freezing behaviour" rather than "flight behaviour" usually seen in response to human presence (Blurton-Jones and Trollope 1968). Kling and Cornell (1971) recorded instances of social behaviour (aggression, threatening behaviour, sexual behaviour and affiliative behaviour) pre-operatively and after bilateral amygdala (and uncus) lesions. The dominance hierarchy was also noted. Post-operatively, the monkeys (independent of social status) had many or all of the symptoms of the KB-syndrome. There were behavioural differences associated with dominance. The most dominant animal remained dominant, a sub-adult female fell in rank and other animals in

the group either fell in dominance or retained their rank. This reinforced the idea that social behaviour must be studied in animals who are members of an established social group with a stable hierarchical system (Kling and Steklis 1976).

Amygdala lesions have also been shown to effect monkey sexual behaviour (another aspect of the KB-syndrome is hypersexuality). This is probably due to the extensive inter-connectivity between the amygdala (centro-medial complex) and the hypothalamus (see Amaral et al 1992 and Chapter III). As in previous reports, amygdala lesions cause increased coprophagia and uriposia, mouthing of non-food objects and decreased fear responses (KB-syndrome). Kling and Dunne (1976) also showed that there was a massive increase in normal and abnormal sexual behaviour after amygdala lesions and when introduced into small social groups (of lesioned and non-lesioned animals). The operated animals performed heightened levels of autofellatio, heterosexual-, homosexual- and self-masturbation and homosexual mounting (males and females). Sexual behaviour was almost non-existent when the lesioned animals were returned to a established large social group (Kling and Dunne 1976). Kling (1968) also studied the effects of giving injections of testosterone to juvenile macaques with amygdalectomies. Kling found that solicited mounting and erections increased between males (before testosterone was given), as did sham-biting, grooming and rough and tumble play. Adult aggressive behaviour was not seen. After testosterone, there was another increase in sham-biting, but a decrease in grooming and other behaviours.

Finally, there is an apparent sex difference in the effects of amygdala lesions in different species of monkeys. In rhesus macaques, the females become the most aggressive, and in some instances are so violent to the males, the attacks on them prove fatal (Kling 1974). The same pattern occurs for stump-tailed macaques, where male aggression and fear responses are drastically reduced after amygdalectomy (Kling 1974). In vervets, female aggression after amygdalectomy is high and directed towards males, who do not appear to retaliate (or know how to respond and therefore, retaliate appropriately).

The amygdala appears to be one area of the primate brain which influences various aspects of social behaviour. It is not known precisely which aspects these are (i.e.

whether deficits in social communication; interpretation or response, fear/danger processing, affiliation or aggression). Kling and Steklis (1976) suggested that the amygdala is part of a functional system intimately involved in the neural coding of social behaviour. The system is comprised of the anterior temporal cortex (temporal pole), which passes information to the amygdala, which in turn outputs to the orbitofrontal cortex. The next two sections will discuss the available evidence that the anterior temporal lobe and prefrontal (orbitofrontal cortex) are part of this circuit.

The original lesions producing the KB-syndrome were directed to the anterior temporal lobes. As stated earlier, lesioning the amygdala alone is sufficient to cause the majority of deficits seen in the KB-syndrome. The cortical parts of the temporal lobe may also contribute to primate social perception and cognition. The evidence for this proposition is clear when discussing the response characteristics of neurons in this region (see below and Chapters VII and VIII). The cortex of the anterior temporal lobe appears to be heavily involved in the visual recognition of complex biological objects, such as hands, bodies and faces (in the ventral cortex, inferotemporal cortex and the superior temporal sulcus; Bruce et al 1981, Desimone et al 1984, Perrett, Rolls and Caan 1982) and the auditory recognition of complex sounds, such as vocalisations (in the dorsal cortex, superior temporal gyrus; Winter and Funkenstein 1973, Ploog 1981, Rauschecker, Tian and Hauser 1995).

Franzen and Myers (1973) lesioned the anterior temporal cortex (leaving the amygdala and hippocampus intact) in rhesus macaques. The lesions had many effects on social behaviour. Early post-operatively, the monkeys displayed increased cage activity, increased approach to human observers (i.e. decreased fear), decreased food intake (maybe due to inappropriate responses to food items) and forced rejection of infants. When the operate monkeys were released into a social group, they showed decreases in dominance and aggressive behaviour (although increased aggression towards humans), decreases in facial expressions, vocalisations and other forms of social communication, decreases in infant affiliation (and usually increased aggression towards infants), increased grooming and increased sniffing/smelling objects. The majority of these deficits can be explained by problems associated with dysfunction of visual processing, such as

not recognising facial expressions appropriately, not recognising individuals (such as alpha male, infant, mother, etc.) or general loss of an object recognition ability.

Raleigh and Steklis (1981) also lesioned the anterior temporal lobe (including some of the temporal pole and the inferior temporal gyrus) in vervet monkeys. They discovered that the amount of grooming initiated by operated animals decreased with increased ablation of the temporal pole, in the overall lesion. They found no other effects of this lesion in the categories they studied.

The final step in the social processing pathway proposed by Kling and Steklis (1976) is the orbitofrontal cortex (part of the prefrontal cortex). This particular area of the brain has received large amounts of attention in the areas of executive functioning, such as memory (Goldman-Rakic 1987), decision-making (Damasio, Damasio and Christen 1996) and motor planning (Passingham 1993). Many investigators have attempted to determine what role the prefrontal and orbitofrontal cortex play in coding social behaviour (or the outputs from anterior temporal cortex and amygdala in the Kling and Steklis 1976 circuit).

Brody and Rosvold (1952) performed the first study to evaluate the effect of prefrontal lesions on social behaviour and social status in monkeys. They found that, as in amygdala lesioned animals, the pre-operative dominance positions of the operated animals were important in determining dominance and social behaviour after the lesion. Three rhesus macaques received prefrontal lobectomies; the most dominant (Back) and two least dominant animals (Alfred and Wizen). Motor activity increased in all three subjects. Back remained dominant after the lesion, as did his social responses. Alfred and Wizen, however, seemed to have reduced fear responses (as seen in their increased attempts to steal food) and did not respond to other's threats. Later observations noted constant fluctuations in the dominance hierarchy of the group, due mainly to increased aggression from the lower subordinate animals towards the previously more dominant animals. Eventually, the levels of aggression returned to normal levels (including downward aggression towards subordinate animals).

Investigations of the prefrontal cortex have looked either at the orbitofrontal cortex or the dorsolateral cortex. Mass and Kling (1975) removed the dorsolateral

prefrontal cortex of stumptailed macaques. They found early effects on social behaviour in the lesioned animals were an increase in aggression and stereotyped pacing. Later effects were increased displacing, threatening, aggression, joining and mounting. The aggression seen post-operatively was inappropriately directed (i.e. from low to high ranking individuals). Singh (1976) also lesioned the dorsolateral prefrontal cortex of rhesus macaques and found an increase in huddling, aggression, self-grooming, exploration of others, stereotypical activity and self-abuse and a decrease in withdrawal, proximity, contact, social grooming, threatening behaviour and vocalisations. (These same behaviours were also seen after orbitofrontal lesions.) A further experiment to test the effects of dorsolateral lesions on social behaviour was performed by Suomi, Harlow and Lewis (1970). Suomi et al tested rhesus monkeys in a social preference paradigm. Here the subjects were placed into the centre of a test apparatus and allowed free time to approach other monkeys (either with or without frontal lobectomies, and of either sex). Subjects with frontal lobectomies (consisting of lesions of the dorsolateral and orbitofrontal cortex) preferred to approach opposite sex monkeys with frontal lesions, but had no preferences for monkeys of the same sex (control or lesion).

The orbitofrontal cortex has been strongly placed in the social processing circuit. Basic emotional reactions (towards human observers in a non-social setting) are compromised after orbitofrontal lesions. Human observers provided the emotional stimuli, by looking directly into the eyes of the subjects. Individually caged rhesus monkeys with these ablations become unaggressive towards human observers and frequently attempt avoidance (by averting the head and eyes, and by lipsmacking; Butter, Mishkin and Mirsky 1968). This is opposite to the laboratory rhesus macaque's usual behavioural reactions towards humans which are aggressive (consisting of threats and occasionally attacks).

These appear to be typical responses when monkeys with orbitofrontal lesions are placed into social situations with conspecifics. Stumptailed macaques reduce the number of threats or aggressive behaviour after orbitofrontal ablation (Miller and Levine 1977). Their activity levels are also reduced, as is grooming. Dominance hierarchy changes because of this. All operates have an overall reduction in activity and an increase

in solitary behaviours (such as self-grooming and reduction in proximity to conspecifics). As with amygdala lesions there is an increase in stereotypical activity (pacing) and mothers with new-born infants ignore them (Myers, Swett and Miller (1973).

Grooming is affected in vervet monkeys after orbitofrontal lesions, possible again due to a increase in solitary behaviour and a reduction in huddling (Raleigh and Steklis 1981). Aggression increases towards human observers in vervets (opposite to rhesus macaques, maybe because of initial differences in aggressive behaviour between the two species). This is substantiated by the finding that there is decreased aggression towards the social group, but also a reduction in the formation of coalitions in females (Raleigh et al 1979).

Aside from lesions of the anterior temporal cortex, Franzen and Myers (1973) also lesioned the orbitofrontal cortex of rhesus monkeys. As with the temporal lesioned animals, there was an initial absence of a fear response directed to the human experimenters. The only activity performed by these animals was stereotypical pacing, and there was also a decrease in food intake. As with the temporal operates, there was a decrease in facial expressions, vocalisations, postures and gestures and a decrease in aggressive behaviour. The decrease in grooming others may again be due to a decrease in general proximity to other group members. The precise similarity of these functional deficits between the orbitofrontal and anterior temporal lesioned animals is convincing evidence for a link in function between these two regions of the monkey cortex.

Peters and Ploog (1976) studied the effects of orbitofrontal lesions on squirrel monkey dominance hierarchies and found that these lesions caused a number of profound deficits in the social behaviour of this New World monkey species. Dominance in this species was determined by the number of head grasps performed by one individual to another (dominant animals perform more head grasps than subordinate animals). After frontal cortex ablation, the number of head grasps was greatly reduced in the most dominant animal, therefore, reducing his position in the hierarchy. Overall, there was a 50% reduction in total social interactions, with reduced fear, competition for food (usually seen as a criteria for dominance) and general reduction in activity levels (with an increase in stereotyped locomotion).

Three other areas of the monkey brain have been studied for possible effects on social interaction. These are the hippocampus, cingulate cortex and superior temporal gyrus (Mirsky 1960, Kawai 1966). Removing the cingulate gyrus of rhesus monkeys appears to have little effect on social behaviour, however, the most dominant animal in the group of lesioned monkey fell after the initial lesion, but recovered after a length of time (Mirsky, Rosvold and Pribram 1957). No other effects on social behaviour were reported by these authors. The hippocampus was originally removed in the Kluver and Bucy (1938, 1939) studies and may make a small contribution to social functioning. Beauregard et al (1995) lesioned the hippocampus (including all subfields and the parahippocampal gyrus) of new-born rhesus macaques, removed from their mothers. The new-borns were tested at 2 months, 6 months and 5-8 years after the lesion for a number of motor and social behaviours. At 2 months, the operates reduced their approach to normal new-borns and were rejected when they did approach. All social interactions between operates and normals were initiated by the controls. After 6 months there were no social abnormalities apparent to the researchers, but at 5-8 years there was an increase in locomotor stereotypies seen after lesions in juveniles and adult monkeys with prefrontal and amygdala lesions.

Other investigators have looked at the time course of brain lesions and the effect on social behaviour. Although brain lesions during the first week of life may have little effect on social processing later in development (as there are assumed to be high levels of functional recovery at this stage of ontogeny), this may not be the case if lesions are performed later in development (Kling 1966, Kling and Green 1967). Harlow (1958) showed that social isolation in rhesus monkeys at this early stage was sufficient to cause pronounced deficits in social behaviour. This effect may be paralleled by lesions to brain structures crucial for this early stage of social development, such as the amygdala. The amygdaloid complex is one of the earliest structures to develop within the temporal lobe (Kordower, Piecinski and Rakic 1992). The two sub-divisions of the amygdala (see chapter III), do not differentiate until later in gestation. This suggests, that although neurons of the amygdala develop early in gestation (embryonic day {E}30 - E50), the

functional organisation may be acquired later in development (allowing for a certain degree of plasticity).

Kling (1966, 1968) has experimented with the idea that there are differences in social behaviour between those adult monkeys who received amygdalectomies as infants and those who received lesions in adulthood. In adult lesioned monkeys the symptoms of the KB-syndrome could be verified as in other studies mentioned above. In infants who received amygdala lesions, however, these behaviours were not seen or were of lesser severity than those seen in adults. These effects have been replicated for rhesus, stumptailed and bonnet macaques (Kling and Green 1967). Some behaviours are spared when damage to the functional systems involved are damaged in early life (Thompson and Towfighi 1976; Thompson, Bergland and Towfighi 1977; Thompson 1981). The separate emotion of fear was found to be prevalent in infant monkeys after amygdalectomy, even though the presence of fear in adult lesioned animals was either reduced or non-existent (Thompson, Schwartzbaum and Harlow 1969).

In summary, it appears that many different lesions localised in the medial and anterior temporal lobe and prefrontal/orbitofrontal cortex cause profound changes in some forms of social and emotional behaviour in monkeys. In the KB-syndrome, the whole of the temporal lobe was lesioned by Kluver and Bucy (1938, 1939), but a number of workers have shown that lesions of the amygdala alone will suffice to produce the same range of deficits in emotion and social processing. Zola-Morgan et al (1991) have also substantiated this view by lesioning either separately or in conjunction, the amygdala and the hippocampus. They found that the hippocampus (which was also lesioned in the initial KB-syndrome studies) appeared to be uninvolved in emotion processing (i.e. did not effect fearful reactions to noxious stimuli) and was only involved in memory processes. The results of Beauregard et al (1995) suggest that emotion may not be processed in the hippocampus, but subtle coding of social behaviour may be performed by this structure. Lesions of the amygdala (Zola-Morgan et al 1991), however, caused disruptions to fear processing (the evidence for difficulties in fear processing in humans is discussed below).

2.2.3 Neurophysiology of the Social Brain

The visual system of primates is an extremely complicated functional network, with an estimated 32 visual areas (Fellman and Van Essen 1991, Young 1992). Basically, the visual system has a hierarchical nature, with two processing streams, dorsal and ventral (Ungerleider and Mishkin 1982, Young 1992). The visual image is processed in increasingly more complex visual areas from the ganglion cells in the retina, lateral geniculate nucleus and the primary visual cortex (area 17, or V1). In the primary visual cortex, the pioneering experiments of Hubel and Wiesel revealed cells which were responsive only to the sight of contours presented at a particular orientation (Hubel and Wiesel 1962). The image is then processed further in extrastriate areas of the brain (for example, V2, V3, V4, MT, FST, parietal cortex). The information of the visual image reaches two areas of interest for this thesis; the superior temporal sulcus (STS) and the amygdala. The physiology and anatomy of the early stages of the primate visual system will not be discussed further. The only information concerning the visual system that is important here, is that visual information reaches the anterior temporal cortex by a particular pathway (see Chapter III) and that the forms of stimuli processed by earlier stages in the pathway are not complex or biological in nature (Perrett and Oram 1993).

The superior temporal sulcus (STS) is a long sulcus running from the parietal cortex, down past V4, to run along side of the inferior temporal cortex to the temporal pole (Seltzer and Pandya 1978). Neurophysiological studies of the STS have found that this cortical area has a primarily visual function, although one of the parcellation areas, called the anterior Superior Temporal Polysensory area (STPa), has been found to have polymodal functions (visual, auditory and tactile, Bruce et al 1981). Cells that have a primary visual function were reported by Gross et al (1972), who recorded in the inferior temporal cortex, specifically finding visually responsive cells in areas TEO and TE (von Bonin and Bailey 1947, see Chapter III for anatomical location). Gross et al were the first to describe, particular cell responses to a complex biological object; a hand. It was not until the late 1970's (Perrett et al 1979) and early 1980's (Bruce et al 1981, Perrett et al 1982) that a systematic study of these types of cell was undertaken. Cells that coded

for a number of biologically important visual stimuli, primarily faces were found by Bruce et al (1981). Bruce et al recorded in the STPa and found that the greatest number of cells were responsive to visual stimuli. They also reported cells responsive to faces (monkey and human), whose firing rate was significantly greater than their response to other objects (such as bars, gratings and non-biological complex objects). These cells were not identity specific as they responded to a wide variety of individual and species' faces and the cells diminished their response when the particular parts of the face were "jumbled", or when the eyes were covered.

Cells in this area were also found to be responsive to other modalities, e.g. auditory and somesthetic stimuli; some required two modalities to be presented together and a small number required three, hence the name "superior temporal polysensory area" (Bruce et al 1981, Hikosaka et al 1988). Polysensory cells may be important in normal social behaviour, as the cells may be crucial to link a facial expression to a vocalisation, or a slap with a particular gesture, for example.

The description of face-responsive neurons was a significant discovery, as the neurological disorder of prosopagnosia has been known for some time. Briefly, this disorder causes the patient to be deficient in recognising previously familiar faces (Damasio 1985, Milders and Perrett 1993).

Continuing work started by Gross et al (1972) and Bruce et al (1981), Perrett et al (1982) reported a systematic analysis of the face-selective cells in the fundus of the STS. These cell responses were 2-10 times as large as the responses to other simple or complex visual stimuli, and other modal forms of stimuli (e.g. auditory). The latency of these cells were between 80 and 160 ms, which was compatible with the notion that the STPa is the next stage of visual processing after the inferotemporal cortex (Oram and Perrett 1992). The response of these cells to faces was found to be constant despite different transformations, including colour, size, distance and orientation (inverted or upright). The cell responses were reduced when the face stimuli was presented in profile and some of the cells were found to be responsive only to particular parts of the face, mainly the eyes.

Perrett and colleagues have continued work on cells in the STS that are responsive to faces, whole and part body motion (Perrett et al 1985b, Oram and Perrett 1994, 1996), static bodies (Wachsmuth et al 1994) and eye gaze (Perrett et al 1985a, Perrett et al 1992). The cells selective to one body, head or eye view have been interpreted as coding "social attention" or the direction in which another's attention lies (Perrett et al 1992). These cells are described in more detail, in Chapters VII and VIII.

Cells responsive to specific identities have also been found in the STS (Perrett et al 1984, Perrett, Mistlin and Chitty 1987) and in the inferior temporal gyrus (Hasselmo, Rolls and Baylis 1989), although the occurrence of these apparently specific "gnostic (grandmother)" cells (Barlow 1972) are rare. The responses of the cells may be tuned to particular facial configurations and not identities per se (Yamane, Kaji and Kawano 1988), or for multiple features in several different horizontal views of the head (Perrett et al 1984, perrett, Mistlin and Chitty 1987). These cells are also discussed more thoroughly, in Chapter VIII.

Cells responsive to different facial expressions are coded in similar regions to the face responsive neurons discussed above; STS (Hasselmo, Rolls and Baylis 1989, Perrett et al 1984, Perrett and Mistlin 1990, Perrett, Oram and Wachsmuth 1993), amygdala (Brothers and Ring 1993), temporal pole (Nakamura et al 1994) and orbitofrontal cortex (Thorpe, Rolls and Maddison 1983). Of all facial expressions, threat faces are represented most frequently at the neuronal level. Cells primarily responsive to threats have been found in the STS (Perrett et al 1984, Hasselmo, Rolls and Baylis 1989, Perrett and Mistlin 1990), accessory basal and medial basal nuclei of the amygdala (Leonard et al 1985, Brothers and Ring 1993), ventral anterior temporal pole (Nakamura et al 1994) and orbitofrontal cortex (Thorpe, Rolls and Maddison 1983). Other facial expressions coded in these regions were grimace (Perrett and Mistlin 1990), yawn (Brothers, Ring and Kling 1990, Perrett and Mistlin 1990). One surprising result was the response of a single neuron to a human smiling face. This response was probably related to the reinforcing nature of the stimulus (human smiling equals more food?), rather than a innate neural response to smiling faces. A behavioural study by Kanazawa (1996) is

suggestive that Japanese macaques may recognise human facial expressions, such as smiling faces.

The preponderance of threat neurons responsive to threat is of evolutionary significance. As discussed previously, being able to respond correctly and swiftly to a threat is extremely beneficial to the animal being threatened. Work performed in human patients with brain lesions, and studies of normal humans with neuroimaging, have complimented the neuronal studies described above (and the lesion studies performed on monkey described above, see also Kling and Brothers 1992).

Populations of cells in the STPa also respond to human bodies as a class of object; with different levels of coding for separate parts of the body (such as the head, torso and legs). These cells tend to respond to either the head presented separate from the rest of the body, the body presented alone or to the whole body (Wachsmuth et al 1994). Ninety-percent of these cells are dependent on perspective view. The majority respond when the head and body are in compatible directions.

All cells within the anterior STS do not just respond to the presentation of faces (i.e the STS is not exclusively an area devoted to processing information about faces). Other investigators have recorded from single units in the STS and found that cells in this area respond to a number of different modalities, as previously described by Bruce et al (1981). Other cells respond to different types of complex visual stimuli (Mikami et al 1994) and others respond to different colours, shapes and patterns (Komatsu and Ideura 1993, Kobatake and Tanaka 1994).

A separate issue raised in a previous section was the development of social responsiveness. Mendelson, Haith and Goldman-Rakic (1981) found that infant rhesus monkeys can discriminate faces by the first week of life, and can discriminate whether a face is directed towards or away from the viewer, by the third week of life. By the third week, infant monkeys also appear to appreciate the emotional significance of the direct gaze (i.e. as a threat); it is learnt that turning away from direct gaze removes an unpleasant experience. Orienting towards faces may be an adaptive mechanism which allows infants to come into contact with the one individual which provides opportunities for survival; the mother. The time course of face discrimination described for rhesus

monkey newborns is different for human newborns. A number of studies suggest that human infants do not tend to orient towards faces until two months of age (see Johnson and Morton 1991 for review). Monkeys also begin to walk around the first day of life, whereas humans tend to begin walking around 9 months old. The development of rhesus monkey behaviour appears to mirror the development of other mammals, i.e. non-human animal infants are less reliant on their mothers than human infants. This has important implications for animals with natural predators, where a highly developed motor system enables greater ease of escape. Processing faces, as distinct visual objects within the first weeks of life, must have been of adaptive value for rhesus monkeys.

Rodman et al (1993) recorded from neurons in the IT and anterior STP of anaesthetised and awake infant rhesus monkeys and found that any visual responses were absent in STPa before 4 months of age, but after this the visual responses were the same as adults (including responses to face stimuli, such as facial expressions and different head views). During this first 4 month period, the infants may have been relying on simpler visual processes which were not coding the details of the face or early face processing occurs in other regions of the brain. It is also possible that Rodman et al missed a number of neurons which were face selective at an earlier age.

The information that reaches the STS and amygdala is already highly processed in terms of form, shape and colour (Perrett and Oram 1993). Neurophysiological studies of the primate amygdala have also elucidated the probable role for parts of or the whole of the amygdala in the recognition, interpretation and production of social behaviour. Rolls and colleagues have recorded in various amygdala nuclei and have reported cells preferentially responsive to the human and monkey face, and other visual forms (Rolls 1981, Rolls 1984, Leonard et al 1985, Rolls 1992). The first set of stimuli shown to monkeys, were visual stimuli which were associated with food reward (Sanghera et al 1979). The cells found to respond to visual stimuli were located in the basolateral amygdala (lateral, medial basal, accessory basal and lateral basal nuclei). Cell latencies for these cells were between 100-190ms which is higher than those visual cells in the temporal cortex (100-150ms, Oram and Perrett 1992). This suggests that cells within the basolateral nuclei in the amygdala are activated after visual processing in the anterior

temporal cortex. This is compatible with the anatomical data (Chapter III) and the lesion data presented above (Kluver and Bucy 1938, 1939, Downer 1961).

The cells responsive to faces found in the amygdala were similar to those found in the anterior STS and inferotemporal cortex (Bruce et al 1981, Perrett et al 1982, Desimone et al 1984). The face selective neurons in the amygdala (12% of the visually responsive neurons) were resposive for monkey or human faces, certain facial expressions and occasionally to more complex stimuli such as pairs of infant monkeys (not responding or a small response to single monkeys). The response of these "complex" neurons was either twice as high as to faces, as to other visual stimuli, with some of the responses five to ten times higher (Leonard et al 1985).

Preliminary studies have already attempted to unravel the neurophysiological basis of processing and interpreting complex visual social signals (Brothers, Ring and Kling 1990, Brothers and Ring 1993). Brothers recorded in the amygdala whilst presenting videofilm of stumptailed macaques performing various visual social signals. The results reported are interesting in the level of complexity with which the cells respond. Unfortunately, the number of cells reported is small, due to special difficulties in recording in the amygdala (Brothers, personal communication). The cells that Brothers and colleagues did report were as selective as neurons within the STS, such as responsive to solicitation for grooming, upward and downward climbing, eye contact, open rather than closed mouths, different identities of humans and monkeys (species differences) and a cell responsive to quadrupedal walking (Brothers, Ring and Kling 1990, Brothers and Ring 1993). The method of testing which Brothers attempted is clearly the way forward in determining what signals evoke responses from single-units in the amygdaloid complex.

Kling has used neurophysiological methods to evaluate the processing of social signals in the amygdala. Kling, however, used free-ranging monkeys performing naturally occurring forms of social interaction; an issue of importance raised from his studies of free-ranging amygdalectomised monkeys (Kling et al 1970). Kling used the method of radiotelemetry. In this technique, the electrodes are permanently embedded in the brain of the monkey and the cell responses were recorded and transmitted as radio waves, for

analysis elsewhere. The monkey was free to move around their environment whilst being continuously recorded from (Kling, Steklis and Deutsch 1979, Kling 1981, Kling, Lloyd and Perryman 1987, Lloyd and Kling 1991). Kling et al (1979) looked at the change in power of delta, omega, alpha and beta EEG waves recorded by radiotelemetry during very particular social interactions. The electrodes were implanted in the basolateral amygdala nuclei. Kling et al found that the highest delta power was seen during passive states of approach, approach with yawn, genital inspection and grooming. The highest power in the omega range was present during passive approach, passive genital inspection, running and chasing, and passive threats. The lowest omega power was seen during other behaviours, such as grooming, sitting together and sleeping.

More recent studies by Kling and colleagues (Kling Lloyd and Perryman 1987, Lloyd and Kling 1991) found a dramatic increase in delta activity when the subject monkey was in the presence of other monkeys, or in particular social interactions, rather than being alone. When the inferotemporal cortex (IT) was lesioned and electrical activity was recorded from the amygdala, Kling et al found that usual high levels of activity to visual stimuli (e.g. human and monkey faces) were decreased when the animal was in isolation. When in the presence of other group members there were no discernible changes.

Perryman, Kling and Lloyd (1987) used visual evoked potentials (VEPs) to test the effect of IT lesions on electrical activity in the amygdala to visual social stimuli. They found that VEPs in the medial basal nucleus of the amygdala were abolished after IT removal, but VEPs were intact in other nuclei. This may be one of the regions which codes the behavioural significance of visual social signals, probably due to it's extensive connectivity to anterior temporal cortex.

Pineda et al (1994) also used event-related potentials to study primate social behaviour. They studied the dominance hierarchy of a group of squirrel monkeys and the effect on ERPs, by presenting certain visual stimuli. Subjects were shown individual monkeys of differing social status, and Pineda et al reported larger N2 amplitudes when the subjects were shown higher-ranking animals. The perception of other's rank in the

social hierarchy can be detected at the neural level, for example in the STS (Young and Yamane 1992).

Amygdala neurons may function in the visual discrimination of complex forms (Nakamura et al 1992). Nakamura presented various types of visual stimuli (including faces) and came to the conclusion that the amygdala is involved in the recognition and evaluation of complex stimuli, and in the short-term storage of these same stimuli. This is probably correct, but the memory functions of the amygdala are likely to include emotional and social information (LeDoux 1987, 1996). Much work has studied the amygdala's role in memory and visual association, but this work will not be discussed here due to lack of space. The following experimental studies discuss the role that the amygdala may play in memory (Mishkin 1978, Gaffan, Murray and Fabre-Thorpe 1993, Wilson and Rolls 1993, Gaffan 1994, Murray and Gaffan 1994). Gaffan, however, has recently suggested that his previous assumptions about the amygdala's role in memory may have been over-interpretative (Gaffan 1995).

It should be mentioned that certain types of social behaviour can be elicited by electrical stimulation of various parts of the amygdaloid complex. Jurgens (1982) caused various types of vocalisations from monkeys by stimulating different areas in the amygdaloid complex. Stimulating the medial basal, lateral basal or accessory basal nuclei elicited purring. Stimulation of the lateral basal, accessory basal and medial nuclei evoked alarm peeps. Stimulation of the medial nucleus was required to cause chattering and groaning vocalisations (see also Robinson 1967).

2.2.4 Psychopharmacology and the Social Brain

The evidence presented above suggests that a number of areas of the brain function in recognising social signals, interpreting the signals and providing a response. The three main areas involved in this process are the anterior temporal cortex, amygdala and orbitofrontal cortex. Further evidence of these areas' involvement comes from studies of sociopharmacology (McGuire, Raleigh and Brammer 1982).

Sociopharmacology is the study of the effects of pharmacological agents (drugs, neurotransmitters, hormones) on social behaviour. It follows that drugs that can pass through the blood-brain-barrier can have an effect on the brain. Effects on particular brain systems can effect particular behaviours. It is safe to presume that, a number of pharmacological agents can effect social behaviour if targeted in the correct brain areas (such as those described above).

Sociopharmacology is an important sub-area of psychiatry, as drug treatments for psychiatric disorders, such as schizophrenia, depression and psychosis have dramatic effects on social behaviour. Social behaviour maybe dysfunctional in these disorders due to a neurotransmitter imbalance. Experiments on monkeys that have revealed precise effects on their social behaviour and status due to drug treatments, will be described here.

Serotonin (5-HT) is an indoleamine (monoamine) neurotransmitter which has a wide range of functions in sleep, depression, eating, sexual arousal, locomotion, pain and aggression (McGuire, Raleigh and Brammer 1982, Carlson 1986). The administration of serotonin precursors or re-uptake blockers, such as tryptophan, 5-hydroxytryptophan (5-HP) and the monoamine oxidase inhibitor, chlorgyline, either produce more serotonin or prevent it being metabolised. Raleigh et al (1980) studied the effects of administration of these drugs and parachlorophenylalanine (PCPA), an inhibitor of serotonin synthesis, on vervet monkey social behaviour. The experiment was split into three stages, baseline (to determine normal levels of social interaction), treatment (where the monkeys were injected with a drug (either tryptophan, PCPA, 5-HTP then PCPA, 5-HTP alone, chlorgyline or saline control) and post-treatment assessment. Tryptophan caused an increase in resting, eating, grooming and approach, a decrease in locomotion, vigilance, solitariness and avoiding others. There appeared to be no change in sexual behaviour, aggression or huddling. PCPA treatment produced some opposites to this scenario (increased locomotion, vigilance, solitariness, avoiding and aggression, but a decrease in resting, eating, huddling, grooming and approach behaviour). Again there was no change in sexual behaviour, suggesting that sexual behaviour is not a simple process dependent on one neural system or neurotransmitter. 5-HTP and chlorgyline treatment increased grooming, vigilance and approach and a reduction in solitary behaviour. Increased

serotonin levels, therefore appear to "promote quiescent and tranquil behaviour" (Raleigh et al 1980), in a social context.

Raleigh then suggested that serotonin may effect social status and dominance through its calming effects (i.e. reduce the most dominant animals' aggressive tendencies). Raleigh et al (1985) administered tryptophan, fluoxetine (a serotonin re-uptake inhibitor; i.e. increase serotonin concentration) and quipazine (a serotonin receptor agonist) to vervet monkeys. Dominance was assessed as a males' success in "dyadic inter-male agonistic encounters" (Raleigh et al 1985). Fluoxetine increased the occurrence of approach, grooming, resting, eating, and huddling, but decreased locomotion, avoidance behaviour, vigilance, solitary behaviour and sexual behaviour. Similar patterns were observed for quipazine (except no increase in huddling, a decrease in submission and no change in sexual behaviour) and tryptophan (no change in sexual behaviour). The behavioural effects were also dependent on social status. Increasing approach (due to fluoxetine) was observed more in dominant, than subordinate animals, whereas decreased vigilance (due to fluoxetine) was observed more in subordinate than dominant animals.

Raleigh et al (1991) also studied the contrasting effects on social behaviour and dominance between tryptophan and fluoxetine, and fenfluramine (an ampetamine derivative which disrupts serotonin storage vesicles and therefore decreases serotonin concentration) and cyproheptadine (a serotonin receptor blocker). Dominance was assessed using the same method as Raleigh et al (1985), but no fluctuations in dominance hierarchy occured throughout the course of the experiment. There were differential effects, however, in the actions of the different drugs. Tryptophan and fluoxetine both increased approach, grooming and proximity, and decreased aggression and locomotion. Fenfluramine and cyproheptadine both produced opposite effects. Fluoxetine and tryptophan also increased male-to-female affiliative behaviours, female coalitions and success in intermale aggression. Again, fenfluramine and cyproheptadine had the opposite effect on these behaviours. Initiation of aggression (by males) and aggression towards females was performed at greater levels by those monkeys who had been treated with fenfluramine and cyproheptadine.

The effects on social behaviour reported here are similar to those seen after orbitofrontal lesions (reduced aggression) in vervets. There are a number of noticeable differences. Grooming behaviour (of others) is decreased by orbitofrontal lesions (Raleigh and Steklis 1981), but is increased after serotonin precursor administration. Grooming behaviour requires an intact orbitofrontal cortex. Increases seen after serotonin treatment suggest that serotonin is acting at the orbitofrontal cortex during this behaviour. This hypothesis also follows for other social behaviours. A different story needs to be written for the effect on aggression. Serotonin treatment causes a decrease in aggression, so does orbitofrontal lesion. Amygdala lesions in free-ranging vervets, however, cause a decrease in aggression (Kling et al 1970), but also a decrease in affiliative behaviours (opposite to the effects of tryptophan and fluoxetine; Raleigh et al 1991).

Brammer, McGuire and Raleigh (1987) attempted to determine where serotonin acts in the vervet brain, using ligand biding of 5-HT_2 to localise concentrations of these receptors. They found high concentrations of receptors in the orbitofrontal cortex (all regions) and the temporal pole, but low concentrations in the amygdala. There were no differences in number of receptors between dominant and subordinate animals. The density of 5-HT_2 receptors can, however, be used to predict effects on social behaviour (see Table 2.2 for a summary).

Table 2.2. Mean number (and SD) of 5-HT2 receptor density in different regions of the vervet monkey brain (n=16). The numbers in the Aggress, Prosocial and Cooperation columns refer to Pearson's correlations betwenn receptor density and acts of social behaviour. Aggress refers to acts of injurious behaviour, Prosocial refers to acts of positive social behaviour and Cooperation refers to acts of cooperative social actions. Data is taken from Raleigh et al (1996). Only those brain areas displaying significant correlations are reported

Brain Area	**Mean (SD)**	**Aggress**	**Prosocial**	**Cooperation**
Posterior Orbitofrontal Cortex	132 (42)	-0.74*	0.86*	0.65*
Medial Frontal Cortex	128 (31)	-0.63*	0.14	-0.23
Temporal Pole	114 (39)	-0.41	0.70*	0.64*
Amygdala	54 (32)	-0.61*	0.63*	0.30
Hippocampus	45 (18)	-0.34	0.63*	-0.23

2.3 Social Behaviour: Human Neurology & Psychopathology

Final evidence that particular brain structures selectively processes social information is derived from studies of human organic brain disorders and psychopathology. One psychopathological disorder which displays prevalent disruptions to social behaviour and communication is autism. Infantile autism was first described by Kanner (1943), as a collection of impairments in social interaction and verbal and non-verbal communication, emotion processing, restricted activities and interests, fear and anxiety and a failure to interpret the actions of others. Autism is not necessarily an impairment of intelligence, as some autistics, known as "idiot savants", have extraordinary talents, such as painting or music. Others have excellent memory and can

remember long lists and tables of numbers, however, an intellectual impairment is common. The social impairments include failure to form attachments with others, failure to take part in pretend play, or inappropriate behaviours such as spontaneous laughter (Mitchell 1996).

Deficits in social forms of communication are good indicators of autism. Face processing is impaired (Hobson 1986, Hobson et al 1988), with autistics having difficulties in recognising emotion in faces where the mouth and forehead have been blanked off. No such difficulty is seen when face identity is processed (although there is a minor impairment in recognising the sex of an individual, Hobson 1986). Davies et al (1994) also studied face perception in autistic and Asberger's syndrome (a mild variant of autism) afflicted children. They found that in contrast to Hobson's results, there were deficits in processing emotion and identity in the high ability autistics, but that this deficit was not face-specific.

Autistic individuals have difficulties in other forms of visual communication. Gaze processing is impaired (see Chapter IX), but only at the level of understanding gaze at a mentalistic level (Baron-Cohen et al 1995, Leekam et al 1997). A major indicator of autism is a lack of joint attention behaviour, such as gaze following, protodeclarative pointing (informative pointing), showing or other forms of "referential communication". Autistic individuals do not direct others attention to objects and events in the environment (Mundy et al 1986) and they do not use pointing gestures (Baron-Cohen 1991). Normal infants, however, readily follow other's gaze (Scaife and Bruner 1975, Butterworth and Cochran 1980, Butterworth and Grover 1989, Butterworth and Jarrett 1991) and pointing gestures (Leung and Rheingold 1981, Blake, O'Rouke and Borzellino 1994) and other forms of joint attention (Morissette, Ricard and Descarie 1995).

An analysis of joint attention skills (protodeclarative pointing and gaze monitoring) and pretend play has been used recently as part of a study of 16,000 18 month old normal infants, in an attempt to evaluate the presence of some of the symptoms of autism (Baron-Cohen et al 1996). The infants were determined to be at risk of being diagnosed as autistic if the infants failed all three tests. Twelve infants failed all

three tests and subsequently ten infants were diagnosed as having autism. After a 3.5 year follow up, all the diagnosed children still had autism.

The deficits in joint attention have been suggested to lead to deficits in theory of mind processing in autism (Baron-Cohen, Leslie and Frith 1985, Baron-Cohen 1994, 1995). The theory of mind deficit was said initially to be derived from poor or absent functioning of the attribution of false belief. Baron-Cohen, Leslie and Frith (1985) adapted Wimmer and Perner's (1983) false-belief task into a special paradigm (the Sally-Anne story) to test for the attribution of false belief in autistics. False belief is the idea that an individual holds a certain belief (i.e. that X is in the box), but that another individual in a different situation may hold a different or incorrect belief. In the Sally-Anne paradigm, the subject is shown a doll (Sally) who places a marble into a basket. Sally then leaves the room and Anne enters the room. Anne moves the marble and hides it in a box. Anne leaves and Sally re-enters the room. The subject is then asked "where will Sally look for the marble?". Normal children (4 1/2 years old) responded by saying that Sally would say that the marble was in the basket (where Sally placed it). Autistic individuals do not appear to appreciate the concept of false belief, as autistics say that Sally would say that the marble was in the box (where Anne hid it). Other tests for deficits in theory of mind tasks in autistic individuals, have looked at the link between seeing, knowing and believing (Leslie and Frith 1988), pretend play, imitation (Whiten 1996b) and language processing (Baron-Cohen 1995, Mitchell 1996). All the above studies found that autistic individuals had deficits in processing.

A number of authors have recently proposed that the temporal and frontal lobes are involved in processing social information, and may be dysfunctional in autism (Heltzer and Griffin 1981, Baron-Cohen and Ring 1992, Brothers and Ring 1992, Bishop 1993, Bachevalier 1991, 1994). Lesions of these brain regions (see previous sections in this Chapter) have similar effects as some of the deficits prevalent in autism. Bachevalier (1991) has compared the effects of neonatal medial temporal lobe lesions in infant rhesus monkeys, with the socioemotional and memory deficits seen in autism. Bachevalier reported striking similarities between the two groups and has suggested that the amygdala, in particular, may be the primary brain area to dysfunction in the autism

disorder (Bachevalier 1994). Others have also suggested a similar scenario (Damasio and Maurer 1978, Heltzer and Griffin 1981, Bishop 1993). Heltzer and Griffin (1981) summarised the similarities between the Kluver-Bucy syndrome and autism thus:

"Deficits in adaptive social behavior along with the lack of recognition of the significance of persons, objects, or events are the very features that are essential to the diagnosis of autism. The profound failure to develop social relationships has been found in nearly all autistic children...The children also show a lack of responsiveness with poor eye contact, and their social development shows a lack of attachment and a failure of bonding...In addition, autistic children demonstrate a preoccupation with and/or stereotyped use of objects without regard for function and have also been widely reported to prefer the use of near receptors such as touch, taste and smell...The children often engage in repetitive sniffing, scratching of surfaces...and scrutiny of visual detail and often explore by putting every new object in their mouth...Hypersexuality is not commonly reported in autism. However, it is interesting to note in this regard that when Akert et al (1961) replicated the Kluver-Bucy syndrome in juvenile monkeys, they found all the main symptoms of the syndrome except the sexual aberrations" (pp. 319-320).

Anatomical, histological and neurochemical differences between the brains of normal subjects and autistic individuals brains, particularly in the temporal cortex and amygdala have been reported (Damasio and Maurer 1978; Bauman and Kemper 1985). The finding that autistic children have been found to have dysfunctions in processing facial emotion and identity (Hobson et al 1988, Davies et al 1994) relate to the findings of cells responsive to emotional expressions and identity within the macaque temporal cortex (Perrett et al 1984; Hasselmo, Rolls and Baylis 1989) in the STS. Autistic children also have a deficit in processing and responding to different communicative gestures, including protodeclarative pointing (Camaioni et al 1994). Cells within the lower bank of the STS (TEa, see next chapter) have been reported to be sensitive to the sight of another individual reaching towards an object (Perrett et al 1989, 1990a, b), which would be comparable to protodeclarative pointing .

Finally, individuals with autism have problems in shifting the focus of their attention, between auditory and visual stimuli (Courchesne et al 1994) and this deficit may be due to a dysfunction of the cerebellar cortex (Courchesne 1997). Cerebellar patients have the same difficulties in shifting attention, but is not known whether such

patients would have the same difficulties as autistics in spontaneously following gaze (Baron-Cohen 1991, 1995).

Recent investigations have began to attempt to map theory of mind functions onto specific areas of the cortex using functional neuroimaging in normal subjects. Baron-Cohen et al (1995) first tested autistic, mentally handicapped and normal children with a list of "mental state" terms, and asked them whether the term had anything to do with thinking. For example, "want, know, pretend" are normal mental state terms, whereas "letter, car, horse" are not. There were significant differences between the three groups, with the autistic group failing to attribute meaning to the majority of mental terms. Second, normal subjects were tested with a larger number of words containing a number of mental state terms. The subjects were asked to raise a finger if the heard a mental state term. In a control condition, the subjects were asked to raise a finger if they heard a word associated with the body, such as the word "brain". During trials, the subject's neural activity was measured using SPECT. The brain region which showed increased blood flow (relative to the frontal polar cortex) during the mental state terms, was the orbito-frontal cortex.

In a related study, Fletcher et al (1995) recorded brain activity using PET while normal subjects performed story comprehension tasks. The tasks either required an attribution of mental states or "theory of mind" in the stories or were "physical" stories or were unconnected sentences. The temporal pole, superior temporal gyrus, posterior cingulate cortex and medial frontal gyrus were active during both types of story, but not during reading of the unconnected sentences. These areas may therefore be connected with the imagery required to understand these stories. When the activation during the "theory of mind" stories were compared with the activation during the "physical" stories, only the left medial frontal gyrus, principally Brodmann's Area 8 was active. The authors therefore suggest, that this area codes for the "mental attribution" part of the story comprehension.

A similar result was obtained by Goel et al (1995) using PET in normal subjects. In their control task, subjects were asked to visualise objects and name them. In the "theory of mind" task, the subjects had to visualise objects, and imagine how others

would use them. This condition could be said to require an understanding of another's perspective (a constituent of theory of mind). In the "theory of mind" task, significantly greater activation was seen in the left medial frontal lobe (Brodmann's Area 9) and the left temporal pole (Brodmann's Areas 21, 39 and 38).

Social behaviour can also be disrupted by organic damage to the structure of the brain, through disease, injury or surgery. The rationale for performing prefrontal lobotomies was derived from the effects of frontal lobe damage on human patients, such as the historical case of Phileas Gage (Damasio 1994, Damasio et al 1994) and monkeys with frontal damage which showed dramatic reductions in aggressive behaviour (see earlier). There are many examples of deficits in social functioning that effect humans after frontal cortex lesions. As stated previously, prefrontal damage in monkeys causes a major disruption of social behaviour. This is also true for human patients who have sustained various forms of damage to the frontal cortex. A patient described by Damasio and colleagues (Eslinger and Damasio 1985; Damasio, Tranel and Damasio 1990; Saver and Damasio 1991), EVR, had sustained bilateral damage to the ventromedial frontal cortex and displayed abnormalities in decision-making in the area of social conduct (or how to behave appropriately in social situations). Damasio found that EVR, when tested on hypothetical social situations was at the same level as normal subjects and control subjects with lesions in different brain areas. If the social situations were "real-life", however, EVR had a large functional deficit, leading to various conclusions that he was sociopathic. The sociopathy was acquired due to the lesion, as previous to his damage EVR had no sociopathic tendencies and behaved normally. Damasio therefore stated three hypotheses concerning EVR's disorder and the function of the ventromedial frontal cortex in social behaviour. First, EVR may not possess knowledge of the appropriate method of social conduct (not substantiated by them as he could perform well in hypothetical situations). Second, and the idea put forward most strongly, is that EVR has lost the ability to analyse and integrate information for use in social behaviour, i.e. EVR has access to the correct social information, but his attribution is impaired. Finally, EVR may not access knowledge of social appropriateness, but could analyse and integrate information successfully.

A collection of human patients have been shown to develop the KB-syndrome (Marlowe et al. 1975, Ghika-Schmid et al 1995). One patient, ES sustained bilateral damage to his temporal lobes and the underlying subcortical structures (including the amygdala) and was found to have symptoms similar to those seen in monkeys with the same damage (Marlowe et al 1975). The patient was unable to recognise a wide variety of common-place objects, which were examined thoroughly when given to him. He could imitate other's use of objects (not seen in monkeys), but failed to recognise familiar individuals (prosopagnosia), his visual orientation was defective and he was unable to determine which were relevant and irrelevant objects. He was remarkably placid and indifferent, and as seen in monkeys, would explore orally all objects within his grasp (including plastic wrapping paper, dog food, ink and faeces). He also had a "reversal of sexual polarity", as he was heterosexual before the temporal damage, but had acutely homosexual tendencies after. The patient described in Ghika-Schmid et al (1995) possessed unilateral damage of the anterior temporal lobe (including the lateral half of the amygdala, but sparing the hippocampus). All symptoms of the KB-syndrome were present in this patient (psychic blindness, hypermetamorphosis, visual agnosia and hypersexuality) suggesting that damage to only one lobe is required to produce the symptoms in humans.

There are also many examples of patients who have sustained amygdala damage who have many of the social processing deficits associated with amygdala damage in monkeys. Patient GR described by Jacobson (1986), received a bilateral amygdalotomy and subcaudate tractotomy to treat her persistent self-mutilation and aggressive behaviour. GR showed disorders in facial recognition (she did not recognise new faces, but did recognise family members and recognised people depending on non-facial characteristics, such as hair style, clothing or glasses), recognising facial expressions, social bonding and affective expression. In all social situations, GR was indifferent and placid, with no anger and therefore failed to create new friendships and emotional attachments. She also experienced difficulties in describing her own emotional state and apart from fear and depression, she didn't know how to "pigeon hole affects into familiar categories" (Jacobson 1986). Finally, she had feelings of remoteness from people and

objects, but was hyperattentive/hyperalert to objects around her, closely inspecting them. The symptoms of this patient are wide-ranging, actually causing profound deficits in normal social functioning, as displayed in monkeys.

The majority of patients are impaired in a small number of problems, not so grossly impaired in social functioning that they cannot function in the social world. A number of patients with amygdala damage have been tested for deficits in face processing (emotion and identity processing, gaze following, etc.). Young et al (1995) described a patient DR who received a bilateral amygdalotomy to treat epilepsy in her temporal lobes. Although, DR did not display any substantial deficits in normal social behaviour, she did perform poorly on a number of facial processing tasks; including recognising familiar and unfamiliar faces, matching unfamiliar faces, gaze direction, and facial expressions. She could recognise highly familiar faces, especially when the faces were known pre-operatively and reject unfamiliar faces. She, however, could not name the familiar faces, but could give their occupation. For example, she would say that the recent Prime Minister John Major was familiar and she could identify his recent job, but she could not name him. She was unimpaired in matching two pictures of unfamiliar people.

Patient DR was also impaired in discriminating between eyes averted and eye contact. A forced-choice paradigm was used where pairs of photographs of faces were presented to the subject. In one-third of the photographs, the head was directed to the viewer, in one-third the head was directed 20^0 to the left and one-third the head was directed 20^0 to the right. Photographs in which the eyes were directed towards the viewer were target faces. Non-target faces were faces in which the eyes were looking away 5^0, 10^0 or 20^0 to the right or left. There were, therefore 6 directions of gaze (5^0, 10^0 and 20^0 left and right) and 3 head views (0^0, 20^0 left and 20^0 right), which produced 18 possible trials. Patient DR was deficient in discriminating eye contact (13 out of 18 correct). This was compared to a mean performance of 16.95 (out of 18 correct) for matched control subjects. DR did not make any errors when the faces were deviated by 20^0 (6 out of 6 correct), but performed worse with smaller deviations; 10^0 (3 out of 6 correct) and 5^0 (4 out of 6 correct).

She was poorly impaired when asked to point at a facial expression which was the same as one of six target expressions (anger, sadness, happiness, disgust, surprise and fear) and she performed badly when asked to name particular expressions (Young et al 1996). The same patient has further difficulties in processing emotion from auditory and speech cues (Scott et al 1997).

A number of other studies in human patients with bilateral damage to the amygdala have found profound deficits in the recognition of facial and vocal emotion, especially anger and fear (Adolphs et al 1994, 1995, Hamann et al 1996). The deficits described were most pronounced when static or motion sequences of emotional expression were presented to the patients and they either had to match the presented picture with a previously presented picture, or they had to name the emotion on the face they were presented with. In none of the studies was facial identity compromised with an impairment of emotion. Morris et al (1996) determined that the recognition deficits for fear are processed by the amygdala in the intact human brain, they presented normal subjects with pictures of varying degrees of emotion from neutral to extreme (using a morphing technique, see also Calder et al 1996 with amygdalectomy patient). The subjects regional cerebral blood flow (rCBF) was measured whilst the subjects made gender judgements of the faces. Fearful faces caused significant activation in the left amygdala and left periamygdaloid cortex. Happy faces, by contrast, caused significant activation in the right medial temporal gyrus, right putamen, left superior parietal lobe and left calcarine sulcus.

These last findings are interesting and surprising when compared to a study of Adolphs et al (1996). They tested a range of brain-damaged patients with emotion recognition tasks, and found that patients with damage to only the left hemisphere were unimpaired in recognising emotion. Damage to the right inferior parietal cortex and the right anterior infra-calcarine cortex caused severe impairments in recognising negative emotions, particularly fear and sadness. There were no deficits in recognising happiness. It may be that patients damaged to the left parietal lobe and left calcarine sulcus may have become impaired in recognising happiness.

Hornak, Rolls and Wade (1996) found that a selection of patients with ventral frontal damage were severely impaired in tests of emotion recognition from faces and voices. The same impairments were not seen across all patients, probably due to differences in the extent of lesion. Again the negative emotions, fear and anger were the expressions most severely defective in recognition.

Patients with amygdala damage have other cognitive impairments, such as problems with memory and attention (Andersen 1978), sensory-somatic cross-modal associations (Nahm et al 1993) and in learning all types of factual knowledge, although, not covert learning (i.e. the link between coding the faces of new individuals and their affective value, Tranel and Damasio 1993).

2.4 Summary

This review has attempted to suggest that non-human primates are a sophisticated, highly social collection of species with a rich social structure. The methods by which Old World monkeys (in particular) communicate with conspecifics and the subtleties of these methods are useful for thinking about human social (non-verbal) communication. The review of the "social brain" literature hopefully shows that some of the subtleties of monkey's social behaviour can be eliminated with discrete lesions of the amygdala, anterior temporal and prefrontal cortices. The effects of these brain lesions in non-human primates appear to parallel the deficits seen after brain damage and psychopathology (especially autism) in humans. The rest of this thesis will look at particular subtleties of monkey social behaviour (such as gaze following, Chapter III), how this is coded by single neurons (Chapters VII and VIII) and how this is represented at the neural systems (Chapter V) and evolutionary levels (Chapter VI).

Chapter III

Architecture of the Primate Social Brain

A. Basic Anatomy

3.0 Introduction

The previous chapter reviewed evidence that three areas of the primate brain may function in coding aspects of social behaviour. The anatomical connections (intra-, cortical, hippocampal and subcortical) of the superior temporal sulcus and amygdala will be reviewed below. The connections of the orbitofrontal cortex are not treated here as the function of this area of cortex in social behaviour is probably not for recognition of social signals which is the area covered by this thesis. The reader is directed to numerous reviews of the connections of the orbitofrontal cortex (Barbas 1988, 1993, Barbas and Pandya 1989, Carmichael and Price 1995, Passingham 1993, Pandya and Yeterian 1990). One of the criteria for an area to be part of the social brain (see Chapter II) was extensive connectivity with other socially-responsive areas. This review of anatomy will help substantiate the evidence provided in the previous chapter. Only anatomical data from macaque species is included in the following review, particularly *Macaca mulatta, M. fascicularis* and *M. fuscata*.

3.1 Superior Temporal Sulcus

The primate temporal cortex lies at the ventral surface of the brain, anterior to the occipital cortex, ventral to the parietal cortex and posterior to the frontal cortex. It is

separated from the parietal and frontal cortices by the Sylvian Fissure (Post-Rolandic cortex), and from the occipital cortex by the occipitotemporal sulcus. The temporal lobe also contains many subcortical structures including the hippocampal formation and amygdaloid complex (see section 3.2).

3.1.1 Architecture

There are four main cortical components of the temporal lobe. The temporal pole (area TG, von Bonin and Bailey 1947 and area Pro, Seltzer and Pandya 1978) lies at the anteriormost end of the temporal lobe. The temporal pole has a multitude of connections (Markowitsch et al 1985, Moran et al 1987), with cortical (visual, olfactory and auditory cortical areas and subcortical structures (e.g. amygdala, thalamus, hypothalamus, brain stem).

Dorsal to the superior temporal sulcus (STS) is the superior temporal gyrus (STG), which is an auditory area (Pandya and Rosene 1993, Jones and Powell 1970). The superior temporal gyrus has been parcellated into various sectors; areas TS1, TS2, TS3, paAlt and Tpt (Seltzer and Pandya 1978, 1994), with each sector connecting to a number of cortical and subcortical areas. The STG is rostral to area PG in the parietal cortex and ventral to the insular cortical areas.

Ventral to the STS is the inferotemporal or inferior temporal cortex (IT). This area is predominantly visual in function (Ungerleider and Mishkin 1982, Mishkin et al 1983, Tanaka et al 1990, Tanaka 1993) and stretches from the anterior temporal pole to area V4t and area V4 in the prestriate visual cortical areas. The cytoarchitectonic areas composing the inferotemporal cortex include areas TE1, TE2, TE3, and TEO (Seltzer and Pandya 1978) or PITd, PITv, CITd, CITv, AITd, AITv (Felleman and Van Essen 1991).

The superior temporal sulcus (STS), runs from the temporal pole (area TG) all the way to the lunate sulcus (LS) and area PG in the occipitoparietal border (von Bonin and Bailey 1947). The STS comprises of lower and upper banks and fundus (depths) of the sulcus. The lower bank consists of areas TEm, TEa and IPa; the upper bank consists

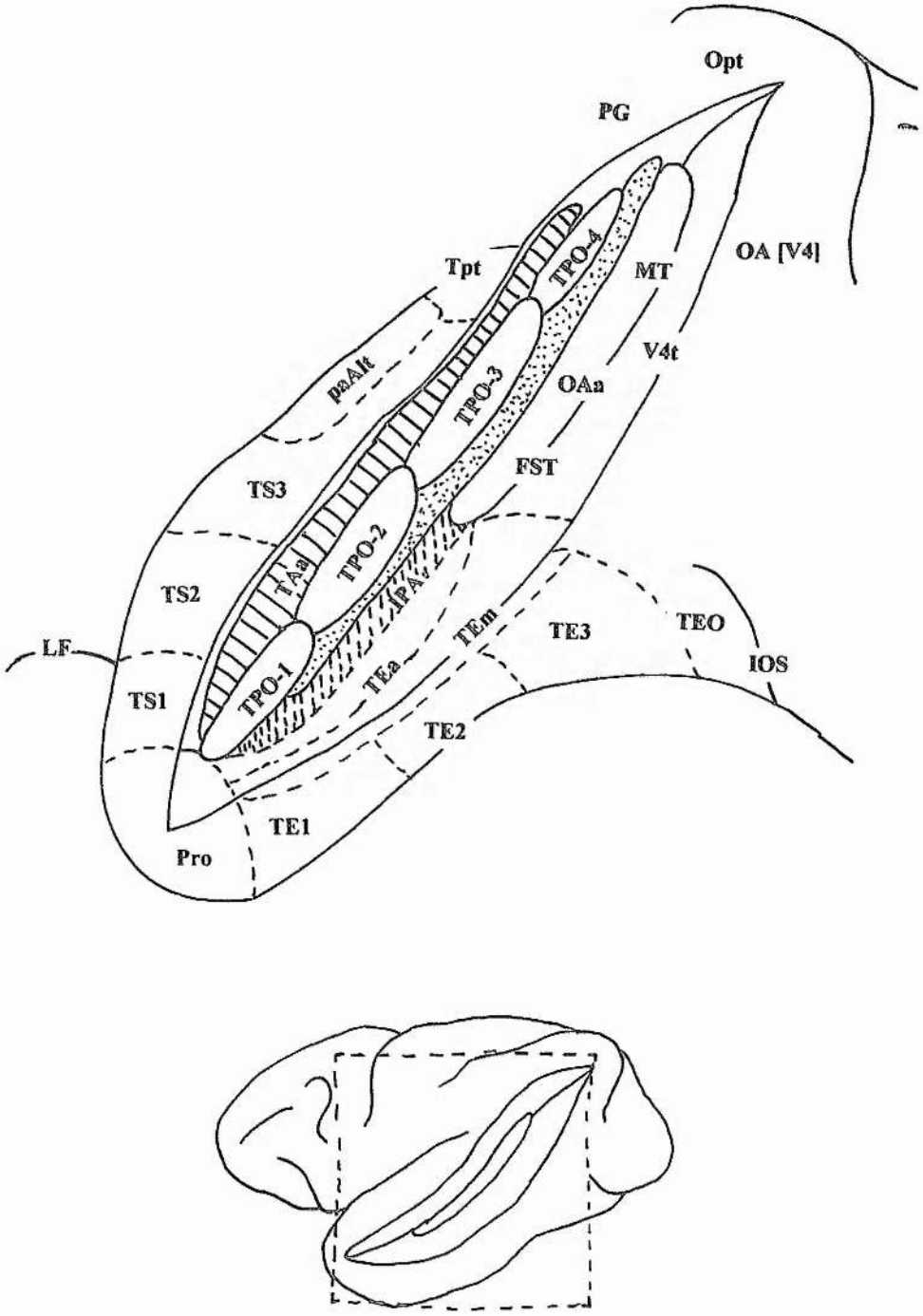
of areas TAa, TPO (1-4) and PGa, and the depth or fundus consists of areas FST, MST, MT and OAa. The anatomical configurations of these areas is shown in figure 3.1. Figure 3.1 also shows how the position of the STS relates to the location of other temporal neocortical areas (Seltzer and Pandya 1978, 1991, 1994).

The upper bank of the STS, comprises of three architectonic zones, area TAa, TPO (1-4) and PGa. Area TAa is located entirely within the upper bank of the STS. The location of TAa can be determined in Nissl stained sections by the predominance of supergranular layers and a single boundary between layers V and VI. Area TPO is medial to area TAa, at the crest of the secondary gyrus, running along the level of the anterior central sulcus, to the caudal lateral fissure. Layer IV is seen as a broad cortical layer in Nissl stained sections of area TPO. There are four compartments to area TPO (1-4), but recently TPO has been subdivided into three sectors (TPOr, TPOi and TPOc; Cuisick et al 1995). At the junction with the depth of the STS is a thin cortical zone called area PGa.. Area PGa is more myelinated than its neighbour area PG.

The lower bank of the STS is architectonically distinct from the rest of the STS. Area TEa is entirely within the lower bank of the STS and architectonically layer IV is thinner than layer IV of area TEm. Area TEm stems the whole of the lower edge of the lower bank of the STS. Layer IV is highly developed, the supragranular cortex is as extensive as the infragranular cortex, and there is a much more diffuse myelination of the inner cortical layers. Area IPa is anterior to area OAa, with a thin, condensed cortical region, which is very poorly myelinated (Seltzer and Pandya 1989).

The depth of the STS consists of the areas, MT, MST and FST. Seltzer and Pandya (1989) name areas MT and FST as OAa. Area OAa is architectonically different from area OA, with a thinner layer IV and a more predominant layer VI, than area OA. The caudal areas of the STS are not considered further here as they are predominantly visual function (processing visual motion) and are extensively connected to the striate and prestriate cortices of the occipital, parietal and temporal lobes (Desimone and Ungerleider 1986a, b, Ungerleider and Desimone 1986, Boussaoud, Ungerleider and Desimone 1990, Hikosaka et al 1990).

Figure 3.1. Upper. Configuration of cortical areas within the superior temporal sulcus (STS), adapted from Seltzer and Pandya (1994). Areas TPO-1, TPO-2, TPO-3, TPO-4, PG and TAa are located within the upper bank of the STS. Areas TEa and TEm are located within the lower bank of the STS. Areas IPa and OAa (MT and FST) are located in the depth (fundus) of the STS. Area Pro is located in the anterior temporal pole, areas TS1, TS2, TS3, paAlt and Tpt area located within the superior temporal gyrus and areas TE1, TE2, TE3 and TEO are located within the inferotemporal cortex. LF is the lateral (Sylvian) fissure and IOS is the inferior occipital sulcus. Area OA (V4) is located in the occipital cortex and area Opt is located within the posterior parietal cortex. **Lower.** Drawing of the lateral (left) side of the rhesus macaque brain showing the position of the STS within dotted line box (left of drawing is anterior, right is posterior).



3.1.2 Inter-areal connections

The STS is separated into three modal regions; the TPO (polysensory cortex), TA (auditory cortex) and TE (visual cortex). The majority of STS connections described in this chapter are to and from the anterior STS. Connections to and from the posterior STS, including MT, FST and MST are not described in detail, and the reader is referred to a number of detailed references (Desimone and Ungerleider 1986, Ungerleider and Desimone 1986, Boussaoud, Ungerleider and Desimone 1990, Hikosaka et al 1990, Morel and Bullier 1990). There is extensive inter-connectivity within the three regions of the STS (upper and lower banks and the depth).

Cells within the rostralmost area of the upper bank of the STS (areas Pro and TPO-1) project to layer I of TPO-1, TPO-2, TPO-3 and rostrally to all layers of IPa, PGa and TAa. Rostral TAa and TPO-1 project cells to all layers of TPO-1, IPa and TAa and layer I of TPO-2, TPO-3 and PGa. TPO-2, caudal TPO-1, PGa and TAa project cells to layer IV of TPO-1 and Pro and all layers of TPO-2 and TPO-3. TPO-4 projects cells to areas medial to TPO (such as the area at the junction between PGa and OAa), IPa and TAa. Cells within TAa, lateral and rostral TPO-3 project to TPO-3, layer I of caudal TPO-4, columnar layer IV of the rostral sub-sections of TPO-1 and TPO-2, PGa and TAa. Rostral and caudal TPO-4, caudal TPO-3, PG and PGa project neurons to areas TPO-2, TPO-3 and PGa. Cells within TAa project diffusely to TPO-4 and the columnar layer of TPO-2 and TPO-3 (Seltzer and Pandya 1989).

Neurons within the sulcal area Pro and the rostralmost TEa and TEm project to layer I of the depth of area IPa, TEa and area OAa. Areas TEa and TEm project afferents to all layers of area Pro, IPa and the rostral portion of areas TEa and TEm, layer I of area OAa. Area TEa projects neurons to columnar layer IV of TEa, paralaminar layers or IPa, layer I of OAa, and TEm. The area within the lower rostralmost segment of the intraparietal sulcus (OAa or MT) projects to TEa, TEm, OAa and IPa; to layer IV rostrally and to layer I caudally. Neurons within area IPa project to all layers of areas Pro, TPO-1 and TEa and layer I of IPa and OAa. (Seltzer and Pandya 1989).

Areas TPO-1 and TEa project to the temporal pole (area Pro), TS1, TS2 and TE1. OAa receives efferents from the upper bank (TPO-1, TPO-2 and TPO-3), the junction of the upper bank and depth (PGa and IPa) and the lower bank (rostral TEa and caudal OAa). The projections to the caudal depth of OAa arise from the supra- and infra-granular layers of TPO-1 and TEa and layer III (supra-granular) of TPO-2, TPO-3, caudal TEa and OAa. Cells within areas Pro, TPO-1, TPO-2, TPO-3, TAa, IPa and PGa project to infra-granular layers of rostral TPO-1 and TPO-2 and supra-granular layers of caudal TPO-1 and TPO-2. The infra- and supra-granular layers of areas TPO-3, TPO-2, TAa and PGa, the infra-granular layer of rostral TPO-1 and the supra-granular layer of caudal TPO-4 project afferents to TPO-2 and TPO-3. The supratemporal plane, TPO-2, TPO-3, TPO-4 and TAa all project neurons to TAa. Cells within the infra-granular layers of Pro, TPO-1 and TPO-2, the supra- and infra-granular layers of TPO-3 and rostral TPO-4 and the supra-granular layers of caudal TPO-4 and PGa project afferents to TPO-4 (Seltzer and Pandya 1989).

Rostral areas TEa and TEm receive efferent projections from the supra- and infra-granular layers of TEa, rostral IPa and rostral TPO-1, caudal PGa and the supra-granular layer of OAa. TEm receives profuse projections from caudal area TEa and OAa, and less dense connections from rostral TEa. The supra- and infra-granular layers of rostral and caudal TEa, the infra-granular layer of rostral TEa and TEm, the supra-granular layer of OAa, UIPa and caudal PGa all project afferents to caudal TEa and TEm on the lower lip of the STS. The infra- and supra-granular layers of TPO-1, TPO-2, TPO-3 and TEa, layer III of PGa and OAa and the infra- and supra-granular layers of IPa project to caudal TEa, IPa and the rostralmost section of OAa. Finally, cells within the infra-granular layer of TEa and the infra- and supra-granular layers of OAa project to OAa (Seltzer and Pandya 1989).

3.1.3 Cortical connections

The STS is extensively connected with a large number of cortical regions. The connections of the different areas of the cortex which connect to the STS will be discussed separately.

a) Frontal lobe connections to STS

Areas within the frontal cortex project to the regions of the STS. The dorsal wing of the prearcuate gyrus and principal sulcus (A46 and A8a) projects afferents to layer IV of the upper bank and fundus of the STS (TPOc, layers I, IV and VI; TPOi, layer IV and TPOr, columnar laminar pattern in layer IV, Cusick et al 1995). Areas Pro, 13, 12, 14, 10, 11 of the orbitofrontal cortex, A24 of the medial cortex and areas 9, 10 and 12 of the lateral cortex project neurons to the temporal pole (area Pro). rostral TPO, PGa and IPa. The lower bank of the principal sulcus (ventral A46) and ventral A6 also project to the supra- and infra- granular layers of rostral TPO, PGa and IPa. The dorsal frontal cortex (A10, frontal pole), rostrodorsal A46, A9, medial areas 10, 14 and 32 project neurons to the mid-portion of TPO, whereas lateral and ventral A46, A12, rostral A8 (the dorsal limb of the arcuate sulcus), medial areas A10 and A24 and the central portion of the orbitofrontal cortex (areas 11 and 12) project to caudal TPO. Dorsal A46 and A8 send connections to rostrocaudal TPO and TAa. The lateral surface of the frontal cortex (upper and lower banks of the principal sulcus, dorsal and ventral A46), dorsal area 6 and medial area 24, all project cells to caudal area TPO (upper bank of the STS), ventral area PG, PGa and the lower bank of the STS (OAa and MT). Cells within the lateral sector of area 12, the ventral portion of the rostral bank of the arcuate sulcus (A8) project to areas TEa and TEm (Seltzer and Pandya 1989).

b) STS connections to frontal lobe

Areas within the upper and lower banks and the depth of the STS project to sectors of the frontal lobe. The upper bank of the STS projects to the following frontal lobe regions. Areas Pro, TPO and TS-1 and TS-2 in the superior temporal sulcus project neurons to the orbitofrontal cortex, proisocortex (area Pro), isocortical areas 11, 12, 13 and 14, areas 25, 32, 14, 10 and 24 on the medial surface and A12 on the lateral surface. Termination within these frontal areas is located within the deep layers of the cortex; lamina IV and the supragranular layers; layer I. Cells within rostral TPO and TAa project to the orbitofrontal cortex (areas 13, 12, 11, 14 and proisocortex), medial frontal cortex (areas 24, 32 and 14) and lateral frontal cortex (areas 12, 10, 9 and ventral A46). Area TPO projects neurons to rostral A10, A46, dorsal A9, principal sulcus (lateral A12), and the supra-granular layer of dorsal A8 and A6 (Seltzer and Pandya 1989).

The lower bank of the STS projects to the following areas of the frontal lobe. Cells within rostral area TEa, TEm, sulcal proisocortex (Pro) and TE1 project cells to the orbitofrontal cortex (area Pro and areas 11, 12, 13 and 14), medial frontal cortex (A24) and lateral prefrontal cortex (principal sulcus, A46, A12 and ventral A8). The projections from the STS terminated within the supra-granular layer of the frontal cortex. Areas TEa, TEm and TE3 project a small cluster of neurons to ventral A12 (Seltzer and Pandya 1989).

The depth of the STS projects to the following frontal cortex areas. Cells within the rostral STS, area IPa and area TEa (encroaching into the lower bank of the STS) project to area Pro, areas 13, 14 and rostral area 11, medial frontal cortex (A9) and lateral frontal cortex (i.e. the midportion of A12 and ventral A46), all terminations within the supra-granular layer (Seltzer and Pandya 1989). Neurons within areas IPa and TEa in the depth of the STS project to area ProM (frontal operculum, Seltzer and Pandya 1991).

.

c) Parietal lobe connections to STS

The inferior parietal lobule including A7a (caudal inferior parietal lobule and upper bank of the caudal most part of the STS) projects to layer IV of TPOi and TPOr

and the columnar layer of TPOc in the STS (Cusick et al 1995). Layers III and V of caudal IPL (area Opt) and layer V of the cingulate gyrus (areas 23, 29 and 30) project neurons to areas TPO-2 and TAa within the upper bank of the STS. Layers III and V of caudal IPL projects neurons to rostral TPO-3 and caudal TPO-2. The apex of the IPL (area Opt) and the lower bank of the IPL (area POa and LIP) project cells to caudal area TPO-3. The medial cortex (areas 31 and PGm) of the parietal lobe, caudal IPL (area Opt), areas PG, area PFG and the lower bank of the IPS (area POa) all project neurons to area TPO-4. The lower bank of the IPS (area POa) also projects neurons to caudal areas TEa and TEm (Seltzer and Pandya 1994). Cells in the rostral inferior parietal lobule project to medial TPO and rostral PGa. Neurons within the middle and caudal inferior parietal lobule and the lower bank of the intraparietal sulcus project to posterior PGa, IPa and the medial sector of TPO (Seltzer and Pandya 1978).

d) STS connections to parietal lobe

The STS projects to areas within the parietal cortex. There are dense projections from Layers V and VI and less dense projections in layer III of areas OAa, TPO-1, -2, -3, PGa and IPa to all layers (I-VI) of area Opt and caudal area PG (area 7a) in the inferior parietal lobule. Dense connections from the supra- and infra-granular layers of TPO-2, TPO-3 and TPO-4 and sparse connections from TPO-1, PGa and TAa to the dorsal area Opt, caudal area PG (A7a) of the inferior parietal lobule. There are dense projections from the supra- and infra-granular layers of TPO-3, PO-4 and PGa and very sparse connections from the infra-granular layers of TPO-2 to caudal and dorsal area PG (area 7a) adjacent to the IPS. Cells within the supra- and infra-granular layers of TPO-4, caudal IPa and PGa project afferents to the mid-portion of the lower bank of the intra-parietal sulcus (PGa, area 7a and LIP). There are dense projections from the supra-granular layer of areas TPO-3 and TPO-4 and scattered projections from the supra- and infra-granular layers of PGa and caudal IPa to rostral and dorsal PGa (areas 7a and LIP). There are connections from the supra-granular layer of OAa and the infra-granular layer of PGa to IPd within the intra-parietal sulcus. Cells within the infra-granular layer of areas TPO-2, TPO-3 and TPO-4 project to the ventral portion of PGm (Barnes and

Pandya 1992). The upper bank area TPO-2, caudal TPO-1, medial PGa and lateral TAa all project cells to the lateral surface of the parietal lobe (PFG, PG and Opt) and the medial surface (cingulate gurus area 23 and 24). Area TPO3 (and TAa) project cells to areas PG, POa of the IPS, areas 23, 31 and PGm. Area TPO-4 projects to area POa (the lower bank of the IPS), areas PGm and A23, and the retrosplenial cortex. Neurons within areas IPa and TEa in the depth of the STS project to area PG within the lower bank of the IPS and the parietal operculum (Seltzer and Pandya 1991).

e) Temporal lobe connections to STS

(i) Superior temporal gyrus

Many areas within the temporal lobe (superior temporal gyrus, inferior temporal cortex, Sylvian fissure, temporal pole and parahippocampal gyrus) have afferent connections to the STS. The crown of the superior temporal gyrus projects to layer IV of TAa, the columnar layer of TPOr and mixed layers of TPOi and TPOc (Cusick et al 1995). Layers III and V of the lateral temporal cortex (areas Pro, TS1-3, paI) project neurons to areas TPO-1 and TPO-2 of the upper bank of the STS. Areas within the rostral superior temporal gyrus (areas Pro, TS1-3), caudal superior temporal gyrus (TS2, TS3, paAlt and Tpt) and the rostral lateral fissure (areas Pro and paI) project to caudal TPO-2 and TAa. Areas within the superior temporal gyrus (areas TS1-3, paAlt and Tpt) project to TPO-3 and TPO-4 (Seltzer and Pandya 1994). Areas Tpt and TAa project neurons to the lateral sector of TPO, TAa and PGa. Cells within areas TS1-3 project to area TAa and TPO. (Seltzer and Pandya 1978).

(ii) Inferotemporal cortex

Supra-granular and infra-granular layers of the inferotemporal cortex (TE1-3, TEm) project to the lower bank of the STS (TEa and TEm). The supra-granular layer of caudal IT (areas TE3 and TEO) projects neurons to caudal areas TEa and TEm. Areas TE1-3, TEO within the inferotemporal cortex project cells to areas TEa, IPa and OAa (FST, Seltzer and Pandya 1994). Areas TEm, TE3 and TEa (dorsomedial inferotemporal

cortex) project cells to rostral STS (TEm, TEa and TE2), whereas cells within areas TE2 and TE3 project to TEa and TEm (Seltzer and Pandya 1978)

(iii) Parahippocampal gyrus

Areas within the ventral temporal lobe (perirhinal A35, areas TF and TL) project neurons to rostral areas of the upper bank of the STS (TPO-1 and TPO-2). Areas 35, TF and TL also project neurons to caudal TPO-2 and TAa (Seltzer and Pandya 1994). Cells within layers III and V of the entorhinal cortex project to caudal TPO-2 and TAa (Seltzer and Pandya 1994, Good and Morrison 1995). Layers III and V of the entorhinal and perirhinal cortices, TF, TH and Tl project neurons to caudal TPO-2 and rostral TPO-3 and layers III and IV of the parahippocampal areas, TH, TF and TL and the prostriate area, project cells to TPO-4. Infra-granular cells within the cortex of the depth of the occipitotemporal sulcus (area TF) project neurons to the lower bank of the STS (TEa and TEm). Parahippocampal areas TF, TH and TL and the prostriate area project neurons to TEa, IPa and OAa (Seltzer and Pandya 1994).

f) STS connections to temporal lobe

(i) Superior temporal gyrus and Sylvian fissure

There are many connections from the STS to the superior temporal gyrus. There are projections from the supra- and infra-granular laminae of TPO-1, supra-granular layers of TPO-2 and rostral TPO-3, TAa, IPa, rostral area PGa and the sulcal component of area Pro to the rostral superior temporal gyrus (TS1 and Pro). There are medium connections from the infra-granular layers of TAa and sparse connections from the infra-granular layers of TPO-4 to caudal superior temporal gyrus including the dorsal and central area paAlt. There are projections from the supra- and infra-granular laminae of areas TPO-1, TPO-2, TPO-3, TAa, rostral PGa and IPa to rostral area TS2. There are dense connections from the supra- and infra-granular layers of TPO-1 and rostral TPO-2, less dense connections from the supra- and infra-granular layers of caudal TPO-2, TPO-3, TAa and less dense connections from sulcal Pro to the central portion of TS1. There

are dense projections from the supra- and infra-granular layers of TAa, scattered projections from the supra- and infra-granular layers of TPO-2 and the infragranular layer of PGa to the rostral sector of area TS3. Cells within the supra- and infra-granular layers of TPO-3 and TAa and the infra-granular layers of TPO-2 and TPO-4 project to the caudal-most portion of the superior temporal gyrus, area Tpt. Cells within the supra- and infra-granular layers of TPO-1, TPO-2 and rostral TAa project to ventral TS2. Cells from the supra-granular TAa and TPO project to dorsal TS2. There are projections from the supra- and infra-granular layers of areas TAa, TPO (-2, -3 and -4) to caudal paAlt. The cells in the supra- and infra-granular layers of TPO (-1, -2 and -3), TAa and PGa project to the ventral portion of TS2. (Barnes and Pandya 1992). Area TPO-1 projects cells to the temporal pole, areas TS1, TS2, the Sylvian fissure (circular sulcus, areas Pro and paI) and the ventral insula. The upper bank area TPO-2, caudal TPO-1, medial PGa and lateral TAa all project cells to the temporal pole, TS (1-3), proisocortex, insula (agranular and dysgranular), circular sulcus (area Pro, paI and ProA) and the supratemporal plane (area paAr), all terminating in layer I. Areas TPO-2 and TPO-3 project neurons to TS (1-3) and the Sylvian fissure (paI, the circular sulcus and the dysgranular insula), whereas TPO-2 and TAa project to areas TS2 (layer IV), TS3 (layer IV), paAlt, Tpt (layer I), the Sylvian fissure (paI, proA and the circular sulcus), KA, paAc and A23 of the cingulate gyrus. Area TPO3 (and TAa) project cells to areas TS2, TS3, paAlt, Tpt, granular insula, areas ProA, reIt (circular sulcus), paAr, KA, paAc. Neurons within areas IPa and TEa in the depth of the STS project to the Sylvian fissure (agranular and dysgranular insula) and the secondary sensory area (SII, Seltzer and Pandya 1991).

(ii) Inferotemporal cortex

The STS projects neurons to areas within the inferior temporal cortex. There are projections from the supra-granular layer of IPa and the supra- and infra-granular layers of TEa, TEm and Pro to area TEa in the lateral bank of the occipitotemporal sulcus. There are connections from the supra- and infra-granular layers of TEa, TEm, IPa and OAa (MT and FST). Cells within the supra- and infra-granular layers of the depths and

lower banks of the STS (areas IPa, TEa, TEm and OAa) project to the boundary between areas TE2 and TE3 (Barnes and Pandya 1992). Rostral TEa and TEm project neurons to layer I of the temporal pole, TE1, TE2, ventral perirhinal cortex (A35b) and the dysgranular insula. Area TEa at the lower rim of the STS projects neurons to layer I of areas TE1-3. The neurons within caudal TEa project to layer I of TE1-3 and TEO. Neurons within areas IPa and TEa in the depth of the STS project to the temporal pole (area Pro) and areas TE1-3 (Seltzer and Pandya 1991).

(iii) Parahippocampal gyrus

Areas within the STS project neurons to the parahippocampal gyrus (areas TH, TF and TL). There are dense connections from the supra- and infra-granular layers of TPO-2, TPO-3 to area TF in the parahippocampal gyrus. Sparse connections from the supra- and infra-granular layers of TPO-1 and TPO-4 to area TF and less dense connections from the supra- and infra-granular layers of PGa and TGa to area TF (Cusick et al 1995). Dense connections from the supra-granular layers of TPO-2, dense connections from the supra-granular and infra-granular laminae of TPO-3, sparse connections from the supra-granular layers of the rostral areas TEa and PGa to area TF. there are dense connections from the supra-granular and infra-granular layers of TPO-2, the infra-granular layer of TPO-3, less dense connections from the supra-granular layers of TPO-1 and TPO-4, sparse connections of the supra-granular layer of PGa, TAa and connections from the sulcal area Pro and IPa to the medial bank of the OTS including area TF. Cells within the supra- and infra-granular layers of TPO-2 and TPO-3, the supra-granular layer of TPO-4 and PGa project to the caudal area Opt (area 7a). There are projections from the infra-granular layer of TPO-2 and the supra-granular layer of PGa, IPa, TEa and OAa (FST) to the midportion of area TF on the medial bank of the parahippocampal gyrus. There are connections from the infra-granular layer of TPO-1 and sulcal Pro and the supra- and infra-granular layers of TPO-3, PGa, TAa and OAa (FST) to the mid-portion of area TF. The cells within the supra- and infra-granular layers

of TPO-2 and TPO-4, PGa, TEa and OAa project to areas TL and TF. Areas Pro, TPO (-1, -2 and -3), IPa and PGa (supra- and infra-granular layers) project neurons to the rostral-most TF, and areas TPO (-1, -2, -3 and -4), PGa, TAa and caudal MT project cells to area TL (Barnes and Pandya 1992). Area TPO-1 projects neurons to areas TH and TL and the perirhinal and prorhinal cortices. The upper bank area TPO-2, caudal TPO-1, medial PGa and lateral TAa all project cells to areas TF, TH and caudal TL. Area TPO-4 projects neurons to areas TF and TH. Rostral TEa and TEm project cells to layer I of rostral TL. Area TEa at the lower rim of the STS projects neurons to the columnar layers of TL and TF. Neurons within areas IPa and TEa in the depth of the STS project to areas TF, TL and the perirhinal cortex (A35, Seltzer and Pandya 1991).

g) Occipital lobe connections to STS

There are some feedback connections from the visual processing areas of the occipital lobe to the sectors of the STS. Layer V of the calcarine retrosplenial cortex projects cells to area TPO-3. The supra-granular layer of the ventral preoccipital gyrus (A19; V4) projects neurons to caudal areas TEa and TEm and the junction between areas TEa, IPa and OAa (Seltzer and Pandya 1994). Neurons within the lateral surface of the occipital lobe; striate cortex (V1) project to area OAa (FST), whereas some neurons within area OA (A19) project to the depth and lower bank of the STS at OAa and to the upper bank at TPO and PGa. (Seltzer and Pandya 1978).

h) STS connections to occipital lobe

Areas within the cortex of the STS project to the occipital cortex. Rostral area TPO-4 projects cells to the upper lip and depth of the calcarhine sulcus (A18 and A19), and layer I of the lateral extrastriate cortex (lunate sulcus, annectent gyrus, dorsal prelunate gyrus and areas V2, V3, V4 and PP). Areas TEa, TEm and rostral OAaproject neurons to layer I of extrastriate areas 19 and V4 within the occipital lobe. (Seltzer and Pandya 1991).

3.2Amygdala

3.2.1 Architecture

The amygdala is a collection of subcortical nuclei located in the medial temporal lobe. It lies in close proximity to the superior temporal sulcus (STS), inferotemporal cortex (IT), parahippocampal areas (entorhinal and perirhinal cortex), insula, hypothalamus and hippocampus (Amaral et al 1992). The amygdala's close proximity to the hippocampus and hypothalamus, and its possible involvement in similar functions, has led to its classification as part of the limbic system (MacLean 1952).

The delineation of subdivisions of the amygdala is a contentious issue. The nomenclature of Amaral et al (1992) will be used here. In an early paper, Johnson (1923) discussed the phylogenetically distinct compartments of the amygdala as the "basolateral" (BL) segment, and the older "corticomedial" (CM) segment. These parcellations are anatomically justified, due to the extensive connectivity of the CM nuclei (the cortical (Co), central (Ce) and medial (Me) nuclei) with subcortical areas such as the thalamus, basal ganglia, hypothalamus and brainstem. The BL nuclei (lateral (L), lateral basal (LB), medial basal (MB) and accessory basal (AB) nuclei), have prolific connections, with sensory and association cortical areas which control sensory and motor behaviour and complex cognitive processing (Amaral and Price 1984, Amaral et al 1992). Other "peripheral" amygdala nuclei include the anterior amygdaloid area (AAA), amygdalo-hippocampal area (AHA), periamygdaloid complex (PAC) and the lateral nucleus of the olfactory tract (LTO).

The two main groups of nuclei in the amygdaloid complex, according to Johnson (1923) are the `centromedial' (consisting of the cortical, medial and central nuclei, and the nucleus of the olfactory tract) and the `basolateral' (consisting of the lateral, accessory basal, lateral basal and medial basal nuclei) groups.

The basolateral (BL) group lies laterally in the brain in close proximity to the temporal association cortex (STS) and claustrum, with the larger number of cortical

connections; with the centromedial (CM) group lying in a more medial position at the inner limits of the brain, and having the majority of subcortical connections. This is seen more easily in Figure 3.2a, a coronal section through the medial temporal cortex of the macaque monkey, showing the various configurations of the specific nuclei. Figure 3.2b shows the relative position of the amygdala nuclei in a photograph of a coronal section through the monkey brain.

The amygdaloid complex also has a wide ranging internal connectivity, leading to the assumption that the different nuclei function differently, but together are functionally integrated (meaning one nuclei affects the outcome of another).

3.2.2 Intra-amygdala nuclei connections

(a) Lateral Nucleus, L -the lateral nucleus of the amygdala is a large nucleic group on the most lateral edge of the amygdala. Its main connections are with the cortical sensory areas, such as the inferior temporal cortex, and the superior temporal gyrus.

Afferents to:- the accessory basal, lateral basal, medial basal, cortical, medial, central, paralaminar nuclei, and the amygdalo-hippocampal area, cortical transition area, anterior amygdaloid area, periamygdaloid cortex, nucleus of the lateral olfactory tract, and the lateral nucleus itself (Nauta 1961; Van Hoesen 1981; Aggleton 1985; Pitkanen and Amaral 1991).

Efferents from:- the accessory basal and central nuclei (Aggleton 1985).

(b) Accessory Basal Nucleus, AB -the accessory basal nucleus is one of the basal nuclei found in the centre of the amygdaloid complex. It is parcelled into two compartments, the magnocellular (mc) and the parvocellular (pc).

Afferents to:- the medial basal, cortical, central, lateral basal, lateral nuclei and the amygdalo-hippocampal area (Nauta 1961; Price and Amaral 1981; Van Hoesen 1981; Aggleton 1985).

Figure 3.2 (b) Photograph of a coronal section through the rhesus monkey brain displaying the amygdaloid complex and the constituent nuclei (lateral nucleus, L; lateral basal nucleus (basal nucleus, magnocellular), Bmg; medial basal nucleus (basal nucleus, parvocellular), Bpc; basal paralaminar nucleus, Bpl; accessory basal nucleus (magnocellular, ABmg and parvocellular, ABpc), AB; cortical nucleus, CO; central nucleus, lateralis, Cl; central nucleus, medialis, Cm; medial nucleus, M; periamygdaloid complex, PAC; entorhinal cortex, EC; rhinal sulcus, rs. Photograph taken from Amaral (1987).

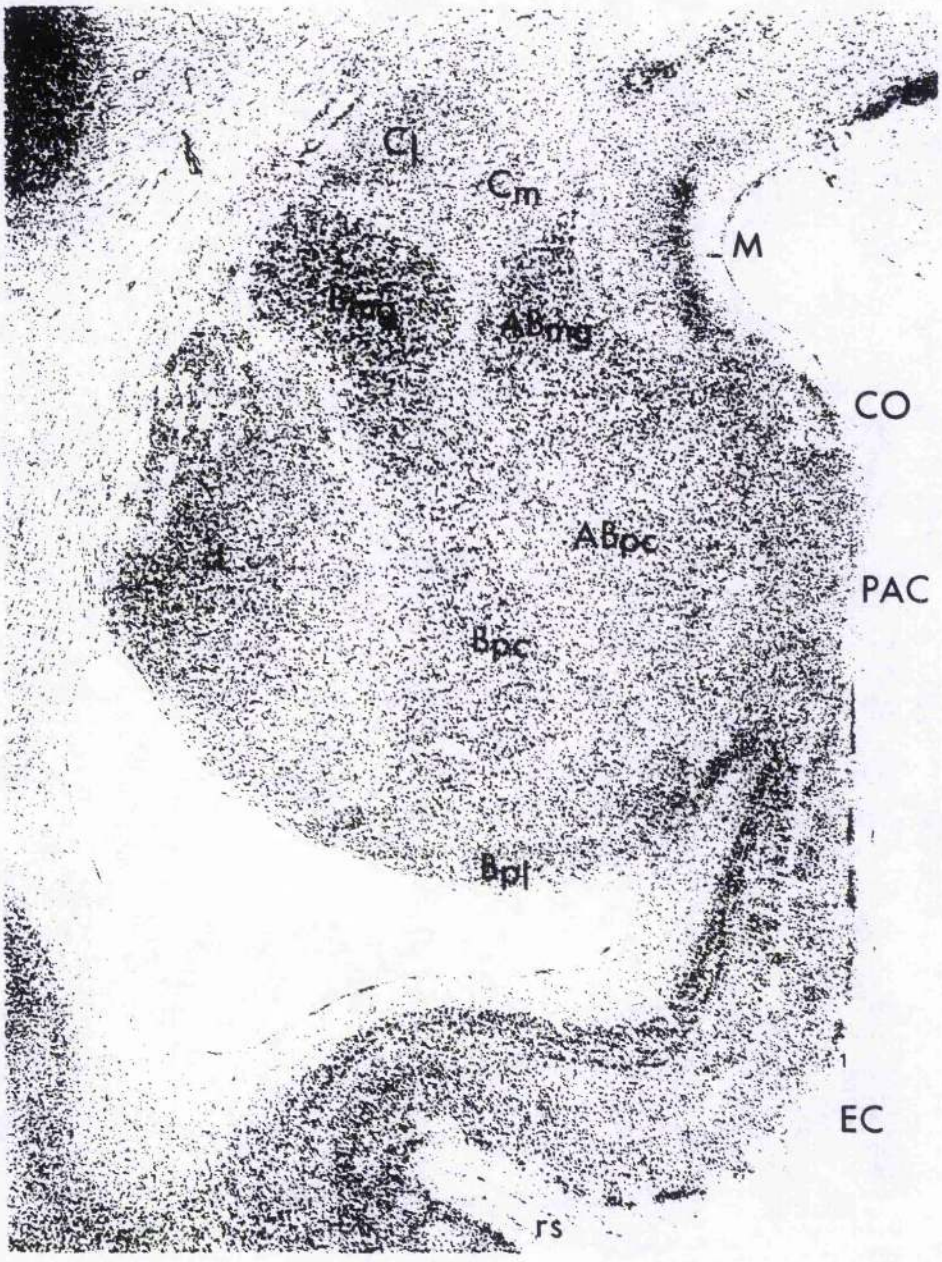
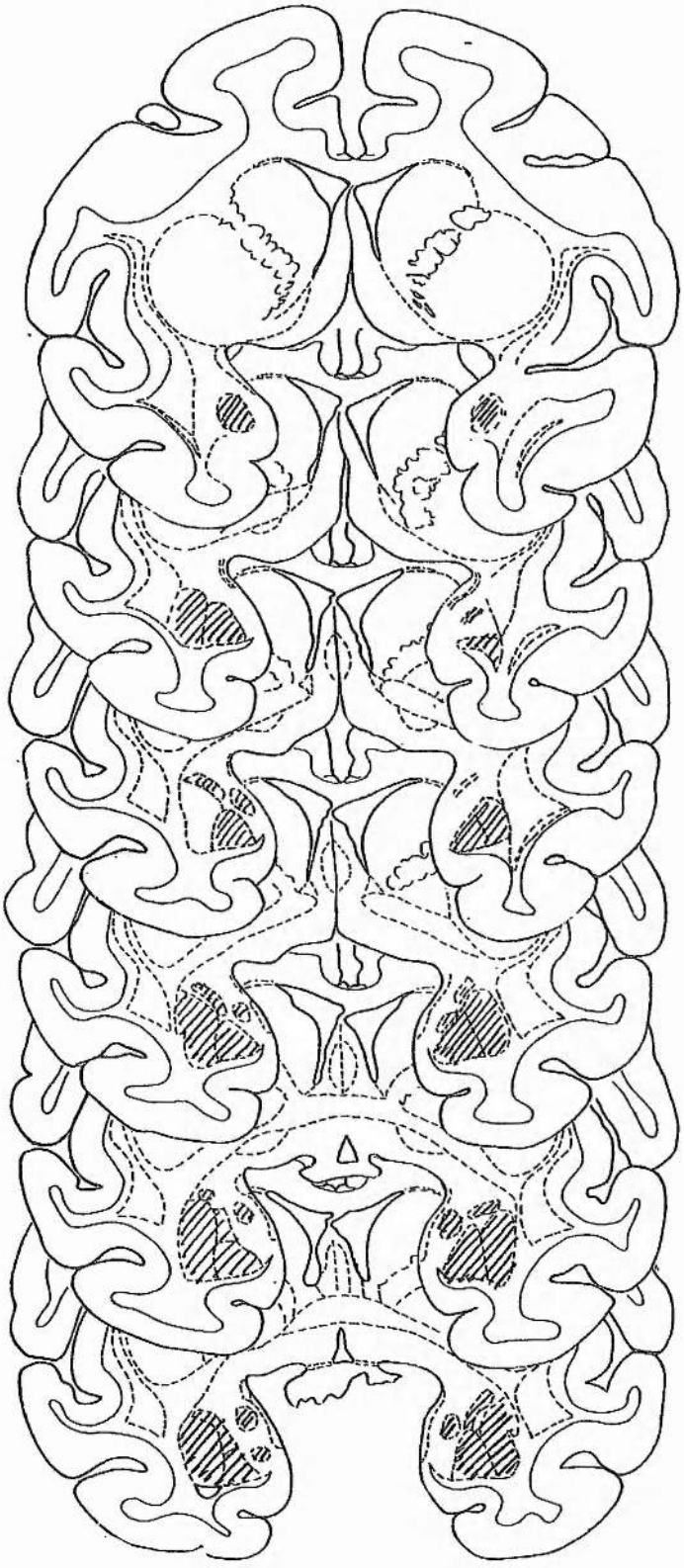


Figure 3.2 (a) Series of coronal sections through the rhesus macaque brain showing the position of the amygdala to cortical and sub-cortical areas. The amygdala is within the hatched area.



Efferents from:- the lateral, central, medial, lateral basal nuclei and the periamygdaloid cortex, and amygdalo-hippocampal area (Aggleton, Burton and Passingham 1980; Price and Amaral 1981; Van Hoesen 1981; Aggleton 1985).

(c) Lateral Basal Nucleus, LB -the lateral basal nucleus is also a component of the basal nucleic group in the centre of the amygdala, next to the lateral nucleus. it is also known as the basal nucleus, magnocellular and intermediate divisions.

Afferents to:- the cortical, medial, central, accessory basal, medial basal nuclei, and the periamygdaloid cortex, amygdalo-hippocampal area and the cortical transition area (Aggleton 1985)

Efferents:- the lateral, medial basal, accessory basal, central, medial nuclei and the amygdalo-hippocampal area (Nauta 1961; Aggleton, Burton and Passingham 1980; Aggleton 1985; Pitkanen and Amaral 1991).

(d) Medial Basal Nucleus, MB -the medial basal nucleus is the final large component of the basal nucleus. It is also known as the basal nucleus, parvicellular division, and is found at the ventral most portion of the amygdala, above the paralaminar nucleus (see below).

Afferents to:- the lateral basal, central, medial basal, cortical, accessory basal, medial nuclei, and the periamygdaloid cortex, cortical transition area and the amygdalo-hippocampal area (Aggleton 1985).

Efferents from:- the lateral nucleus and the amygdalo-hippocamapal area and the periamygdaloid cortex (Aggleton 1985).

(e) Medial Nucleus, Me -the medial nucleus is a component of the corticomedial complex (Johnson 1923), found in the medial part of the brain, close to the lateral nucleus of the olfactory tract.

Afferents to:- the cortical, accessory basal, lateral basal and central nuclei, and the cortical transition area, periamygdaloid cortex and the amygdalo-hippocampal area (Aggleton, Burton and Passingham 1980; Van Hoesen 1981; Aggleton 1985).

Efferents from:- the lateral, lateral basal, medial basal and central nuclei (Aggleton 1985; Pitkanen and Amaral 1991).

(f) Central Nucleus, Ce -the central nucleus is also part of the corticomedial complex, in the medial forebrain. In more anterior portions of the brain, it develops from the anterior amygdaloid area. It has a high connectivity with the deeper subcortical areas, such as the medulla and pons.

Afferents to:- the cortical, lateral, accessory basal, medial basal, lateral basal, central nuclei and the cortical transition area, periamygdaloid cortex and the amygdalo-hippocampal area (Aggleton, Burton and Passingham 1980; Price and Amaral 1981; Aggleton 1985).

Efferents from:- the lateral basal, accessory basal, lateral and medial nuclei and the periamygdaloid cortex (Price and Amaral 1981; Van Hoesen 1981; Aggleton 1985; Pitkanen and Amaral 1991).

(g) Cortical Nucleus, Co -the cortical nucleus is the final main nucleus comprising the corticomedial nucleic group. The cortical nucleus blends with the periamygdaloid nucleus, and some investigators deem the cortical nucleus and the periamygdaloid nucleus to be one and the same. It is separated into anterior and posterior parcels.

Afferents to:- the medial and periamygdaloid cortex (Amaral et al 1992).

Efferents from:- the central, lateral, lateral basal, accessory basal, medial basal and medial nuclei and the periamygdaloid cortex (Price and Amaral 1981; Van Hoesen 1981; Aggleton 1985; Pitkanen and Amaral 1991).

(h) Periamygdaloid Cortex, PAC -the periamygdaloid cortex is the area of cortex lying on the most medial portion of the amygdala, ventral to the cortical nucleus, and dorsal to the cortical transition area. The periamygdaloid cortex is therefore neither cortex, or amygdala (in the true sense).

Afferents to:- the periamygdaloid cortex projects to the medial basal, accessory basal, medial, central and cortical nuclei (Van Hoesen 1981; Price and Amaral 1981).

Efferents from:- the periamygdaloid cortex receives connections from the lateral, medial basal, lateral basal, accessory basal, medial and central nuclei (Price and Amaral 1981; Aggleton 1985; Pitkanen and Amaral 1991).

(i) Cortical Transition Area, CTA -the cortical transition area lies underneath the periamygdaloid cortex, at the transition point with the entorhinal cortex and other hippocampal structures.

Afferents to:- the afferent connections of the cortical transition area are unknown at this time (if they do indeed exist).

Efferents from:- the lateral, lateral basal, medial basal, central and medial nuclei (Aggleton 1985).

(j) Paralaminar Nucleus, PL -the paralaminar nucleus is a long, thin nucleus running along the ventral edge of the basal nucleic groups. It is sometimes thought to be a superficial part of the medial basal nucleus, but has a vastly reduced connectivity.

Afferents to:- the afferents of the paralaminar nucleus are also unknown at the present time.

Efferents from:- the lateral nucleus (Aggleton 1985; Pitkanen and Amaral 1991).

(k) Amygdalo-Hippocampal Area, AHA -this area as the name implies, is the transition area between the hippocampus and the amygdala . It is therefore only found at more posterior portions of the amygdala, on the dorsoventral side.

Afferents to:- the lateral basal, accessory basal and the medial basal nuclei (Aggleton 1985).

Efferents from:- the lateral, lateral basal, accessory basal, medial basal, central and medial nuclei (Price and Amaral 1981; Aggleton 1985).

(l) Anterior Amygdala Area, AAA -the anterior amygdaloid area as the name states, is situated at the more anterior portions of the amygdala, and is sometimes confused with the central nucleus.

Afferents to:- the afferent projections of the anterior amygdaloid area haven't been discovered at this present time.

Efferents from:- the lateral and central nuclei (Aggleton 1985; Pitkanen and Amaral 1991).

(m) Nucleus of the Olfactory Tract, NOT -there is some debate as to whether the nucleus of the olfactory tract is part of the amygdala. It is included here for completeness, due to it's location close to the rest of the amygdaloid groups. It is thought to be part of the amygdala, as the amygdala was once thought to have an primary olfactory function.

Afferents to:- the afferents of the NOT are also not known at the current state of knowledge.

Efferents from:- the lateral nucleus (Aggleton 1985; Pitkanen and Amaral 1991).

The many different nuclei of the primate amygdala have a large variety of cortical, subcortical, hippocampal and internal connections. This suggests that the amygdala should not be analysed as a whole structure when the connectional data for each particular nuclei is so radically different, and the connections of individual nuclei to many functionally distinct areas of the monkey brain (see below).

3.2.3 Cortical connections

The amygdaloid complex has been shown to have many varied and extensive connections with the temporal cortex and temporal pole. Efferent projections from the amygdala to the temporal pole originate in the corticomedial and basolateral amygdaloid groups. The following nucleic groups project to the temporal pole (Area TG); accessory basal, lateral basal, medial basal, lateral, periamygdaloid complex, central, cortical, medial nuclei and the cortical transition area and the anterior amygdaloid area . Area TG also sends many afferents back to the amygdala; to the lateral, accessory basal, lateral basal,

medial basal, periamygdaloid complex, cortical, medial and central nuclei (Herzog and Van Hoesen 1976; Aggleton, Burton and Passingham 1980; Turner, Mishkin and Knapp 1980; Amaral and Price 1984; Markowitsch et al 1985; Iwai and Yukie 1987; Moran, Mufson and Mesulam 1987). Therefore, the basal nuclei and a few other nuclei have a reciprocal connectivity with the temporal pole. The temporal pole may have such a large connectivity with the amygdaloid complex due to the close proximity, and similar functions, such as vision (Nakamura et al 1994), to other heavily amygdala-connected temporal cortical structures, such as the STS.

More posterior areas of the temporal cortex also have connections with the amygdaloid complex. The inferior temporal cortex (Area TE of von Bonin and Bailey 1947) has a wide plethora of connections with the amygdaloid complex, which has been demonstrated by a large number of anatomical investigators. The inferior temporal cortex projects heavily to the lateral, lateral basal, accessory basal, medial basal, and central nuclei (Whitlock and Nauta 1956; Herzog and Van Hoesen 1976; Aggleton, Burton and Passingham 1980; Iwai et al 1987). This is a diffuse, general projection, which is also reciprocated from the amygdala to the inferior temporal cortex; from the lateral basal, lateral, accessory basal, cortical, and medial basal nuclei, and periamygdaloid cortex (Nauta 1961; Amaral and Price 1984; Iwai et al 1987; Baizer, Desimone and Ungerleider 1993).

There are also connections between specific areas of the inferior temporal cortex and the amygdala. Anterior temporal cortex (Area TEa) projects to the lateral, central, lateral basal, medial basal, accessory basal nuclei and the anterior amygdaloid area (Turner, Mishkin and Knapp 1980; Iwai and Yukie 1987). The amygdala (lateral basal, accessory basal, medial basal, lateral and periamygdaloid cortex) also projects to Area TEa (Iwai and Yukie 1987; Yukie et al 1990). Posterior temporal cortex (Area TEp) also has connectivity with the amygdaloid complex; projecting to the lateral and lateral basal nuclei (Turner, Mishkin and Knapp 1980; Iwai and Yukie 1987). This is reciprocated from the lateral basal, medial basal, lateral and accessory basal nuclei (Iwai and Yukie 1987; Yukie et al 1990).

The areas of the temporal association cortex which have been deemed primarily visual or polysensory in function, for example the superior temporal sulcus, and the areas situated within the STS, such as MT\MST\FST and STPa, also have a rich connectivity with the amygdala. The lateral and lateral basal nuclei project to the ventral bank of the STS (Amaral and Price 1984), and the STS (rostral, and both banks) projects to lateral basal, lateral, medial, central and medial nuclei (Herzog and Van Hoesen 1976; Aggleton, Burton and Passingham 1980). Areas MT\MST do not project to the amygdala, but there is an efferent connection from the amygdala; from the lateral and lateral basal nuclei (Iwai and Yukie 1987)

Areas of the temporal cortex which are primarily auditory in neurophysiological function are also connected to the amygdala. The superior temporal gyrus (Area TA) sends afferents to the lateral basal, lateral, accessory basal, and central nuclei (Herzog and Van Hoesen 1976; Aggleton, Burton and Passingham 1980; Turner, Mishkin and Knapp 1980; Mizuno et al 1981, Iwai and Yukie 1987). Efferent connections from the amygdala to Area TA arise from the lateral basal, lateral, accessory basal, and cortical nuclei (Nauta 1961; Amaral and Price 1984). Therefore, there is also a reciprocal arrangement between the superior temporal gyrus and the lateral, lateral basal and accessory basal nuclei.

Finally there are connections between parahippocampal temporal areas, TH and TF and the amygdala. There is a fairly strong afferent connection to the lateral nucleus from Areas TF and TH (Aggleton, Burton and Passingham 1980).

Although there is a substantial connectivity between the temporal association cortex and the amygdala, there is also a smaller projection from the amygdala to the occipital cortex, and more importantly the primary visual areas. The only nuclei in the amygdaloid complex which has a direct connection with the visual areas of the occipital lobe and the occipitotemporal border is the lateral basal nucleus. The lateral basal nucleus afferent travels to the striate cortex (Primary Visual Cortex, Area 17, Area V1) (Mizuno et al 1981; Amaral and Price 1984; Iwai and Yukie 1987); Area V2 (Area 18) (Iwai and Yukie 1987); and Area V4 (Iwai and Yukie 1987).

The parietal cortex also has a small association with the amygdala, with the accessory basal, lateral basal and medial basal nuclei sending afferents to Area 7 of the parietal cortex (ventral bank of the rostral intraparietal sulcus) (Amaral and Price 1984), and the lateral nucleus receiving an efferent connection from Area 7 (Aggleton, Burton and Passingham 1980). There is also a connection from the lateral basal nucleus to the premotor area (Area 6) (dorsomedial to the superior limb of the arcuate sulcus), but no connection from Area 6 to the amygdala (Avendano, Price and Amaral 1983, Amaral and Price 1984). There has also been noted to be a pathway from the lateral basal and medial basal nuclei to posterior parietal cortex (Baizer, Desimone and Ungerleider 1993).

Many of the areas which are constituents of the macaque frontal cortex are interconnected with the amygdaloid complex. The frontal eye field, Area 8, receives efferents from the lateral basal nucleus (Jacobson and Trojanowski 1975; Barbas and DeOlmos 1990). Area 9 projects to the central, lateral, medial basal, lateral basal and accessory basal nuclei of the amygdala (Leichnetz and Astruc 1977) and the medial nucleus (Aggleton, Burton and Passingham 1980). The lateral basal nucleus projects to Area 9, therefore there is a reciprocal connection between the lateral basal nucleus and Area 9.

The frontal pole (area 10) also has a major projection to the amygdala from the basal (accessory basal, lateral basal and medial basal) nuclei (Jacobson and Trojanowski 1975; Porrino, Crane and Goldaman-Rakic 1981; Amaral and Price 1984), and pathways from Area 10 to the central, lateral, medial basal, lateral basal, accessory basal and medial nuclei (Leichnetz and Astruc 1977; Aggleton, Burton and Passingham 1980). The frontal cortical areas 11 and 12, on the ventral surface of the prefrontal cortex, also have a degree of connectivity with the amygdala, with the lateral basal, medial basal, accessory basal projecting to Area 11, and the basal, lateral and cortical nuclei projecting to Area 12. Area 11 sends an afferent projection to the medial nucleus (Aggleton, Burton and Passingham 1980), but Area 12 has no afferent connections to the amygdala.

The orbitofrontal cortex (Area 13) sends and receives neural connections with the amygdala; the accessory basal, lateral basal, medial basal, lateral and cortical nuclei project to Area 13 (Nauta 1961; Barbas and DeOlmos 1990); and Area 13 projects to

lateral and medial nuclei (Aggleton, Burton and Passingham 1980). Other frontal cortical areas have an association with the amygdala. Area 14 projects to the lateral and accessory basal nuclei (Aggleton, Burton and Passingham 1980), and the accessory basal, lateral basal and medial basal nuclei all project afferent nerve fibres to Area 14 (Amaral and Price 1984; Barbas and DeOlmos 1990).

The cingulate gyrus (Area 24) located in the medial part of the brain, also has extensive connections with the basolateral groups of the amygdala. The lateral basal, medial basal and accessory basal nuclei all project afferents to the cingulate gyrus (Porrino, Crane and Goldman-Rakic 1981; Amaral and Price 1984); and the cingulate gyrus projects back to lateral (Aggleton, Burton and Passingham 1980) and lateral basal (Pandya, Van Hoesen and Domesicj 1973; Pandya, Van Hoesen and Mesulam 1981).

Other frontal areas that have connections with the amygdaloid nuclei are Area 25 (where the lateral, lateral basal, medial basal, accessory basal and cortical nuclei project to, and the medial nucleus from, Area 25); Area 32 (where the lateral basal, accessory basal, medial basal, cortical nuclei and anterior amygdaloid area project to Area 32-Amaral and Price 1984; Barbas and DeOlmos 1990); Area 45 (which receives input from the basal nuclei (Amaral and Price 1984) and Area 46 (which receives efferent connections from the accessory basal, lateral basal and medial basal nuclei-Barbas and DeOlmos 1990).

The principal sulcus also distributes inputs and outputs to and from the amygdala; the lateral basal nucleus projects to it (Jacobson and Trojanowski 1975); and the principal sulcus projects back to the lateral basal and medial nuclei (Aggleton, Burton and Passingham 1980). There are further connections between the amygdala and the frontal cortex, with a connection between the frontal granular cortex and its efferent from the lateral basal nucleus (Jacobson and Trojanowski 1975). Also the superior prefrontal dimple sends afferents to the lateral basal and medial nuclei (Aggleton, Burton and Passingham 1980), and the subcallosal gyrus sends afferents to the lateral basal, medial and accessory basal nuclei (Aggleton, Burton and Passingham 1980).

The final area of the macaque cortex which has extensive connectivity with the amygdaloid complex is the insular cortex. The insular cortex has three components; the

agranular, granular and granular cortices. The accessory basal, medial basal, cortical and lateral basal nuclei project to the agranular cortex (Mufson, Mesulam and Pandya 1981; Mufson and Mesulam 1982; Friedman et al 1986), and the agranular cortex projects to the anterior amygdaloid area, medial, cortical, medial basal, accessory basal, lateral and lateral basal nuclei (Mufson, Mesulam and Pandya 1981).

The granular insular cortex has an efferent connection from the medial basal, accessory basal, lateral basal and cortical nuclei (Mufson, Mesulam and Pandya 1981; Mufson and Mesulam 1982); and sends an afferent to the lateral nucleus (Friedman et al 1986).

The final part of the insular cortex, the dysgranular cortex, sends a connection to the anterior amygdaloid area, medial, cortical, central, medial basal, accessory basal, lateral basal and lateral nuclei (Mufson, Mesulam and Pandya 1981, Friedman et al 1986). The accessory basal, medial basal, lateral basal, lateral and cortical nuclei project afferents to the dysgranular cortex (Mufson, Mesulam and Pandya 1981; Mufson and Mesulam 1982; Friedman et al 1986).

More general connectivity with the insular cortex can also be seen in the macaque monkey. The lateral, lateral basal, accessory basal, medial basal nuclei, and the amygdalo-hippocampal area, and the periamygdaloid cortex all project diffusely to the insular cortex; and the insula also projects diffusely to the anterior amygdaloid area, lateral basal, accessory basal, medial basal, cortical, lateral and central nuclei (Turner, Mishkin and Knapp 1980; Mufson, Mesulam, and Pandya 1981; Mesulam and Mufson 1982b; Mufson and Mesulam 1982; Friedman et al 1986).

A substantial amount of the projections that leave and enter the amygdala, arise and terminate in the hippocampal formation. In this report, the hippocampal formation is taken to include the hippocampus (including the stratum moleculare and subfields CA1, CA2, and CA3), entorhinal cortex (A28), prorhinal cortex (Prl), perirhinal cortex (A35), subiculum (A36), parasubiculum (A49), presubiculum (A27), prosubiculum (Pro) and the rhinal sulcus. This nomenclature follows that designated by Van Hoesen and Pandya (1975).

The entorhinal cortex (Area 28) receives efferents from the amygdala, and projects afferents to the amygdala. It projects to the lateral, accessory basal, paralaminar nucleus, anterior amygdaloid area, periamygdaloid cortex, medial basal, central, medial and cortical nuclei (Insausti, Amaral and Cowan 1987; Aggleton, Burton and Passingham 1980); and receives from the lateral, lateral basal, accessory basal, medial, central nuclei and the periamygdaloid cortex (Saunders and Rosene 1988a; Aggleton 1985; Aggleton, Burton and Passingham 1980).

The prorhinal cortex (Prl) receives many connections from the amygdala; lateral basal, accessory basal, medial and central nuclei, and the prorhinal cortex projects to medial basal and lateral basal nuclei (Aggleton 1986). The perirhinal cortex (A35) also connects to the amygdaloid complex; with the lateral basal, medial basal, cortical, lateral, and accessory basal nuclei (Saunders and Rosene 1988a; Amaral and Price 1984; Aggleton 1986) projecting to it, and Area 35 projects to the medial basal, and lateral basal nuclei (Herzog and Van Hoesen 1976; Aggleton 1986).

Other non-hippocampus areas of the hippocampal formation include the subiculum, prosubiculum, presubiculum, parasubiculum and the rhinal sulcus. The accessory basal, medial basal, cortical nuclei and the cortical transition area project to the prosubiculum (Saunders and Rosene 1988a; Aggleton 1986); and the prosubiculum projects to the medial basal, accessory basal, lateral, lateral basal nuclei and the cortical transition area and the periamygdaloid cortex (Aggleton 1986; Saunders and Rosene 1988a). The subiculum receives efferents from the accessory basal, lateral basal, medial basal, lateral, central nuclei and the cortical transition area (Saunders and Rosene 1988a; Aggleton 1986; Amaral and Price 1984), and sends afferents to the medial basal, lateral, lateral basal, paralaminar nuclei and the cortical transition area (Aggleton 1986; Rosene and Van Hoesen 1977). The parasubiculum (A49) and the presubiculum (A27) both receive inputs from the lateral basal nucleus (Aggleton 1986), and the rhinal sulcus sends outputs to the lateral basal, lateral, accessory basal and medial nuclei (Aggleton, Burton and Passingham 1980).

3.2.4 Subcortical connections

Aside from the connections with the cortex and the hippocampal formation, the amygdala has a wide and extensive connectivity with many subcortical structures. The amygdala was originally thought as being an olfactory structure and the links with the olfactory areas are quite pronounced. The olfactory bulb sends an afferent to the Co (Turner, Gupta and Mishkin 1978) and the olfactory tubercle sends afferents to the AB, LB, MB and L nuclei (Nauta 1961; Aggleton, Friedman and Mishkin 1987). The LB, MB, AB, L, Ce, Me and Co nuclei and the AAA and AHA project to the olfactory tubercle areas; Tol 1, 2, and 3 (Nauta 1961; Price and Amaral 1984; Russchen, Amaral and Price 1985; Russchen et al 1985; Aggleton, Friedman and Mishkin 1987).

The subcortical (afferent and efferent) connections of the individual amygdala nuclei are summarised in Table 4.1. The references describing each connection are also displayed in the table.

Subcortical Nucleus	*Afferent (input)*	*Efferent (output)*	*References*
Hypothalamus			
Ventromedial nucleus	Ce, LB	AAA, AB, Ce, Co, MB, Me, LTO, PAC	1, 4, 6, 8, 10
Dorsomedial nucleus	AB, Ce, L, LB	Ce, Co, Me	1, 6, 10
Mamillary nuclei	AB, L, LB	Ce	4, 6, 10
Lateral hypothalamic area	AB, Ce, L, LB	AAA, AB, Ce, Co, L, LB, Me	1, 4, 6, 8, 10
Dorsal hypothalamic area	Ce	N/A	10
Posterior hypothalamic area	L, LB	N/A	6
Lateral tubercle nucleus	LB	N/A	10
Basal Ganglia			
Caudate nucleus (head, body & tail)	AB, LB, MB, PAC	Whole amygdala	1, 9, 11
Caudate nucleus (body)	AAA, AB, Co, L, MB	N/A	9, 11
Caudate nucleus (tail)	AAA, AB, Co, L, LB, MB, Me	N/A	9, 11
Putamen	AB, Ce, Co, L, LB, MB, Me, PAC	AB, Co, L, LB, MB	7, 9, 11, 12
Globus pallidus	AAA, AB, Co, MB	AB, AHA, Ce, Co, LB, L, MB, Me, PAC, PLN	11, 12
Ventral pallidum	AB, LB, MB	AB, AHA, Ce, Co, CTA, L, LB, MB, Me, PAC, PLN	11
Claustrum	AB, L, LB, MB	AB, Co, L, LB, MB	7
Nucleus accumbens	AB, AHA, Co, L, LB, MB	AB, Ce, L, MB	7, 11, 12
Basal Forebrain			
Substantia innominata	AB, L, LB, MB	AB, Co, L, LB, MB	1, 2, 7, 11
Nucleus basalis of Meynert	AB, AHA, Ce, Co, L, LB, MB, Me, PAC, PLN	AB, AHA, Ce, Co, CTA, L, LB, MB, Me, PAC, PLN	10, 11
Nucleus of the diagonal band of Broca	Ce	AAA, AB, Ce, Co, L, LB, MB, Me	1, 7
Anterior commissure	AB, LB, MB	AB, LB, MB	7, 11

Table 3.1. Macaque amygdala connections with subcortical areas (thalamus, hypothalamus, basal ganglia, basal forebrain, midbrain, pons and medulla). Abbreviations and references are at the bottom of the table.

Subcortical Nucleus	*Afferent (input)*	*Efferent (output)*	*References*
Thalamus			
Midline nuclei, nucleus centralis, nucleus medialis dorsalis, midline nucleus reuniens, medial pulvinar nucleus, nucleus paraventricularis, nucleus parafascicularis, habenula, nucleus anterior medialis, nucleus alaris, nucleus rotundus, nucleus limitans, lateral dorsalis nuclei, nucleus parataenialis, nucleus reuniens ventralis, nucleus nterventralis, nucleus subparafascicularis pars magnocellularis and parvocellularis, nucleus peripeduncularis	AB, AHA, Ce, CTA, L, LB, MB, Me, PAC		3, 6, 10
Nucleus anterior medialis, nucleus centralis, nucleus alaris, nucleus rotundus, nucleus parafascicularis, nucleus paraventricularis, nucleus reuniens, ventral anterior nucleus, nucleus paracentralis, nucleus subfascicularis, nucleus centrum medianum, nucleus medianum, habenula, medial pulvinar nucleus, midline nuclei, medial geniculate nucleus, central medial nucleus, peripeduncular nucleus, interpeduncular nucleus		AB, Ce, Co, LB, Me	1, 3, 8

Subcortical Nucleus	Afferent (input)	Efferent (output)	References
Midbrain, Pons & Brainstem			
Substantia nigra	AB, L, LB, Ce	AAA, Ce, dorsal amygdala, L, LB	1, 4, 6, 8, 11
Ventral tegmental area	AB, Ce, L, LB	Ce, whole amygdala	4, 6, 8, 10
Peripeduncular nucleus of the midbrain		AB, L, LB, MB	1, 5
Nucleus of posterior commissure	Ce		10
Nucleus cuneiformis	Ce		10
Central gray	Ce	AB, whole amygdala	1, 10
Periamygdaloid gray		Whole amygdala	1
Raphe nuclei	Ce	Ce, Co, L, LB, Me	8, 10
Nucleus medialis annuli aqueductus		Whole amygdala	1
Mesencephalic trigeminal nucleus		Whole amygdala	1
Parabrachial nuclei	Ce	Ce, Co, Me, PAC	8, 10
Mesencephalic nucleus of the fifth nerve	Ce		6, 10
Nucleus of the tractus solitarius	AB, Ce, L, LB		6, 10
Spinomedullary border	Ce		6, 10
Area postrema, area subpostrema	AB, L, LB		6
Dorsal motor nucleus of the vagus	AB, L, LB		6
Reticular formation	Ce		10
Pontine nuclei	Ce		10
Locus coeruleus	Ce	Ce, Co, L, LB, Me	8, 10

Abbreviations:

AAA, anterior amygdaloid area; AB, accessory basal nucleus; AHA, amygdalo-hippocampal area; Ce, central nucleus; Co, cortical nucleus; CTA, cortical transition area; L, lateral nucleus; LB, lateral basal nucleus; Me, medial nucleus; MB, medial basal nucleus; PAC, periamygdaloid complex; PLN, paralaminar nucleus; N/A, not available.

References:

1. Aggleton, Burton & Passingham '80, **2.** Aggleton, Friedman & Mishkin '87, **3.** Aggleton & Mishkin 1984, **4.** Amaral, Veazey & Cowan '82, **5.** Jones et al '75, **6.** Mehler '80, **7.** Nauta '61, **8.** Norita & Kawamura '80 **9.** Parent, Mackey & DeBelluille '83, **10.** Price & Amaral '81, **11.** Russchen, Amaral & Price '85 **12.** Russchen et al '85

Chapter IV

Architecture of the Primate Social Brain

B. Connectional Analysis

4.1 Introduction

The brain is a metabolically expensive organ, on par with the gastro-intestinal tract in levels of energy consumption (Aiello and Wheeler 1995). It would be false economy for the brain to contain redundant connections between areas which are not directly functionally associated. For example, the primary visual cortex (V1) is not directly connected to the primary motor cortex (A4), as there is no functional requirement for this connection to exist. It would therefore seem reasonable to suggest, that the brain is designed to enhance the product of its activity; behaviour. For example, to enhance function, the lowest possible number of synapses required to transmit information from A to E would be used. The simplest route for information to be communicated A to E (including all areas in between), is via A to B to C to D to E. Information would not get passed from A to G to F to G to H to B to C to D to E, as an example; unless there is a precise, functional reason for this to occur (as may be required by parallel distributed processing; Rumelhart and McClelland 1986).

The brain is often described as a complex processing organ. Is the complexity of the brain's anatomy (and connectivity) reflected in the complexity of the brain's function? Sambrook and Whiten (1997) have recently discussed what complexity is in cognitive and behavioural science and suggested that complexity lies between orderedness and randomness. For example, a checkerboard is ordered, a random-dot stereogram is randomised (in one eye), but a fractal pattern is complex. Can the brain be thought of

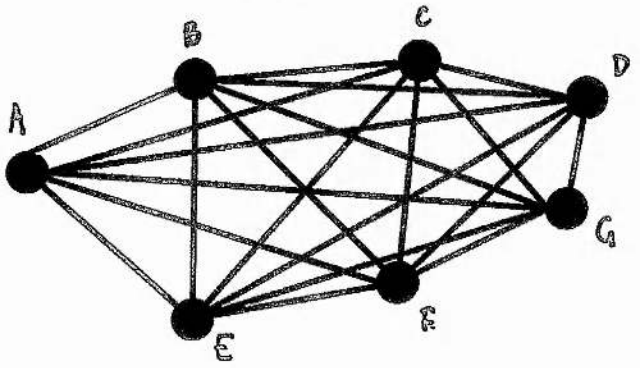
being complex, random or ordered (see Figure 4.1)? As stated earlier, it is unlikely that the brain is random as this would be wasteful from a metabolic sense and impossible from the standpoint of evolution. The primate brain has evolved to solve specific social and environmental problems; there would be no requirement for random connections (without a functional purpose). Is the connectivity of the brain ordered? If this was the case, every brain area would be connected to every other brain area. The brain could not function at this level, as integral processing stages may be missed by passing information by the fastest route from A to B. As A and B would be directly connected, the information would not have passed through the required processing stages. Behaviourally, this could be fatal to the animal housing the "ordered brain". It would therefore follow, that the connectivity of the brain is complex. Primate behaviour would also suggest this, due to the complexity of some of its manifestations (Sambrook and Whiten 1997, Sambrook 1995).

As reviewed in Chapter II, a large number of investigations have studied social complexity and the possible areas of the primate brain which may be involved in controlling this level of complexity. One area which was highlighted in these studies was the amygdala. From Chapter III, we know that the amygdala is a collection of subcortical nuclei located in the medial temporal lobe. It lies in close proximity to the superior temporal sulcus (STS), inferotemporal cortex (IT), parahippocampal areas (entorhinal and perirhinal cortex), insula, hypothalamus and hippocampus (Amaral et al 1992). The amygdala's close proximity to the hippocampus and hypothalamus, and its possible involvement in similar functions, has led to its classification as part of the so-called limbic system (MacLean 1952, although see arguments against the limbic-system concept in LeDoux 1996).

The delineation of subdivisions of the amygdala is a contentious issue. The nomenclature of Amaral et al (1992) will be used here. A number of early papers, Johnson (1923) and Crosby and Humphrey (1941, 1944) discussed the phylogenetically distinct compartments of the amygdala as the "basolateral" (BL) segment, and the older "corticomedial" (CM) segment. These parcellations appear anatomically justified, due to the extensive connectivity of the CM nuclei (the cortical (Co), central (Ce) and medial

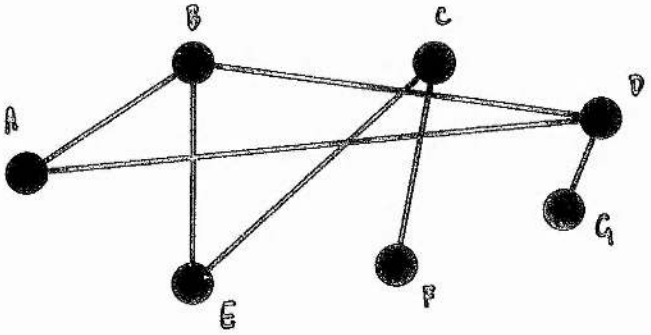
Figure 4.1: Diagrams of a hypothetical brain system (areas A-G) with connections between areas. **(a)** *Ordered pattern of connections*, i.e. every area is connected to every other area. If information needs to travels from area A to area G, there are an infinite number of pathways by which the information can travel, depending on the levels of processing required. The simplest route is directly from area A to area G. **(b)** *Random pattern of connections*, i.e. some areas are connected, whilst some are not. Information, again is required to travel from area A to area G, but there are a finite number of routes through which the information can travel. The simplest route is area A to area D to area G. The reduction in the number of routes required may also reduce the levels at which information can be processed. **(c)** *Complex pattern of connections*, i.e. each area connects to a small number of other areas (in this example, a maximum of two), which allow information to be processed through many stages. There is a precise, finite number of processing steps to pass information from area A to area G (area A to area B to area C to area D to area E to area F to area G).

(a) ORDERED (infinite)



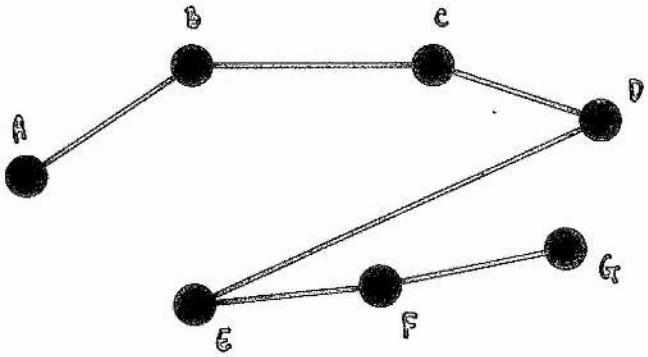
Possible pathways: A-G or A-B-C-D-G or A-E-F-B-G etc.

(b) RANDOM (finite; imprecise)



Possible pathways: A-B-D-G or A-D-G or A-B-E-C-G

(c) COMPLEX (finite; precise)



Possible pathways: A-B-C-D-E-F-G

(Me) nuclei) with subcortical areas such as the thalamus, basal ganglia, hypothalamus and brainstem. The BL nuclei (lateral (L), lateral basal (LB), medial basal (MB) and accessory basal (AB) nuclei), have prolific connections, with sensory and association cortical areas which control sensory and motor behaviour and complex cognitive processing (Amaral and Price 1984, Amaral et al 1992). Other "peripheral" amygdala nuclei include the anterior amygdaloid area (AAA), amygdalo-hippocampal area (AHA), periamygdaloid complex (PAC) and the lateral nucleus of the olfactory tract (LTO). Comparative and evolutionary issues concerning the functions of these two parts of the amygdala are discussed and analysed in the next chapter.

Do the individual connection patterns of the primate amygdala nuclei relate to the functions of the amygdala in social cognition, and can this information be investigated by analysing the connections of the amygdala with separate neocortical areas? The statistical technique of non-metric multidimensional scaling (NMDS) has recently been adapted to determine the connectional similarities of particular brain regions (Young 1992, 1993, Young, Scannell et al 1995). NMDS allows visualisation of the global organisation of sets of interconnected objects. The similarities between these sets of data are then displayed as 2D or 3D geometric figures, showing relative distances between data points as computed in multidimensional space (Young and Harris 1993). Most brain areas are not inter-connected. A recent addition to the application of the NMDS method in this area is data transformation and conditioning, which reduces the impact of large numbers of non-connections between brain areas in the database matrix (Young, Scannell et al 1995).

The NMDS method was employed by Young (1992) to analyse the cortico-cortical connections of the monkey visual system, and the results substantiated the findings of neuroanatomy, animal lesion studies and human neuropsychology (Ungerleider and Mishkin 1982, Felleman and Van Essen 1991, Goodale and Milner 1992), that the cortical visual system was separated into two distict processing streams (dorsal and ventral-Young, Scannell et al 1995). NMDS also indicated that information from the streams has the opportunity to re-converge in the rostral region of the temporal lobe; area STP and in the frontal cortex; area 46. NMDS provides an objective method of

analysis of brain connection data, which can be used in formulating subjective opinions about the relationships between brain anatomy and behavioural function.

Previous NMDS analysis of the amygdala's cortical connections (Young and Scannell 1993) treated the amygdala as a single cohesive structure (see Figure 4.2). Given the large number of separate amygdala nuclei, it is likely that the particular nuclei have different functions. It is also likely that, individual amygdala nuclei have distinct connectivity patterns, which can be analysed using NMDS. This study treats the amygdala as a collection of separate nuclei, and analyses the connections of each nucleus separately. Early anatomical and cytoarchitectural studies suggested that the amygdala was also separated into two larger sub-areas, the BL and CM complexes (Johnson 1923). This study used NMDS to attempt to evaluate objectively whether the definition of two nuclear groups was justified using connectivity data. The study also attempted to define the relationships between amygdala nuclei and cortical systems (particularly the temporal and frontal cortex), thought to be involved in social processes.

4.2 Methods

4.2.1 Anatomical nomenclature

The cortical area nomenclature was taken from Felleman and Van Essen (1991), with the exception of the auditory cortical nomenclature which was taken from Galaburda and Pandya (1983), and Pandya and Yeterian (1985).

The amygdala nuclei nomenclature and parcellation was taken from Amaral et al (1992). The lateral nucleus of the olfactory tract and the paralaminar nucleus were not included here due to their very sparse cortical and intrinsic amygdala connections, and their marked reduction in size and probably function in Old and New World monkeys and apes (Stephan et al 1987). The parcellation of cortical areas in an idealised monkey brain, was developed from Pandya and Yeterian 1985, Felleman and Van Essen (1991), and Preuss and Goldman-Rakic (1991), and is displayed in Figure 4.3a, b, and the configuration of the amygdala nuclei is displayed in Figure 4.3c.

Figure 4.2: Output plot for macaque amygdalo-cortical connections analysed using NMDS, without the use of data transformation methods or separating the amydala into constituent parts. Taken from Young and Scannell (1993).

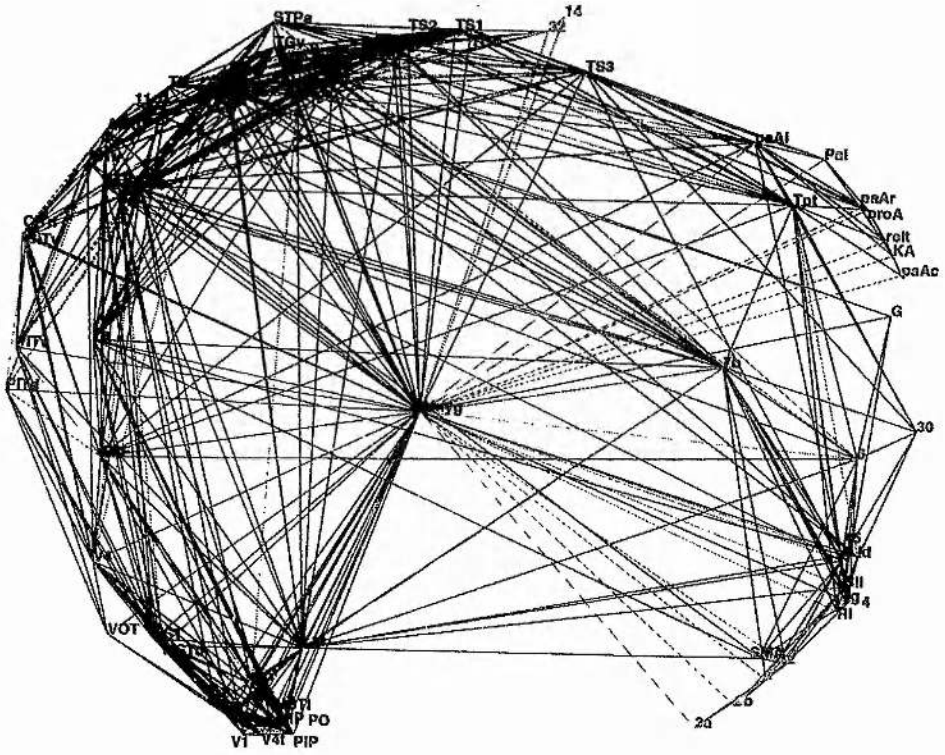
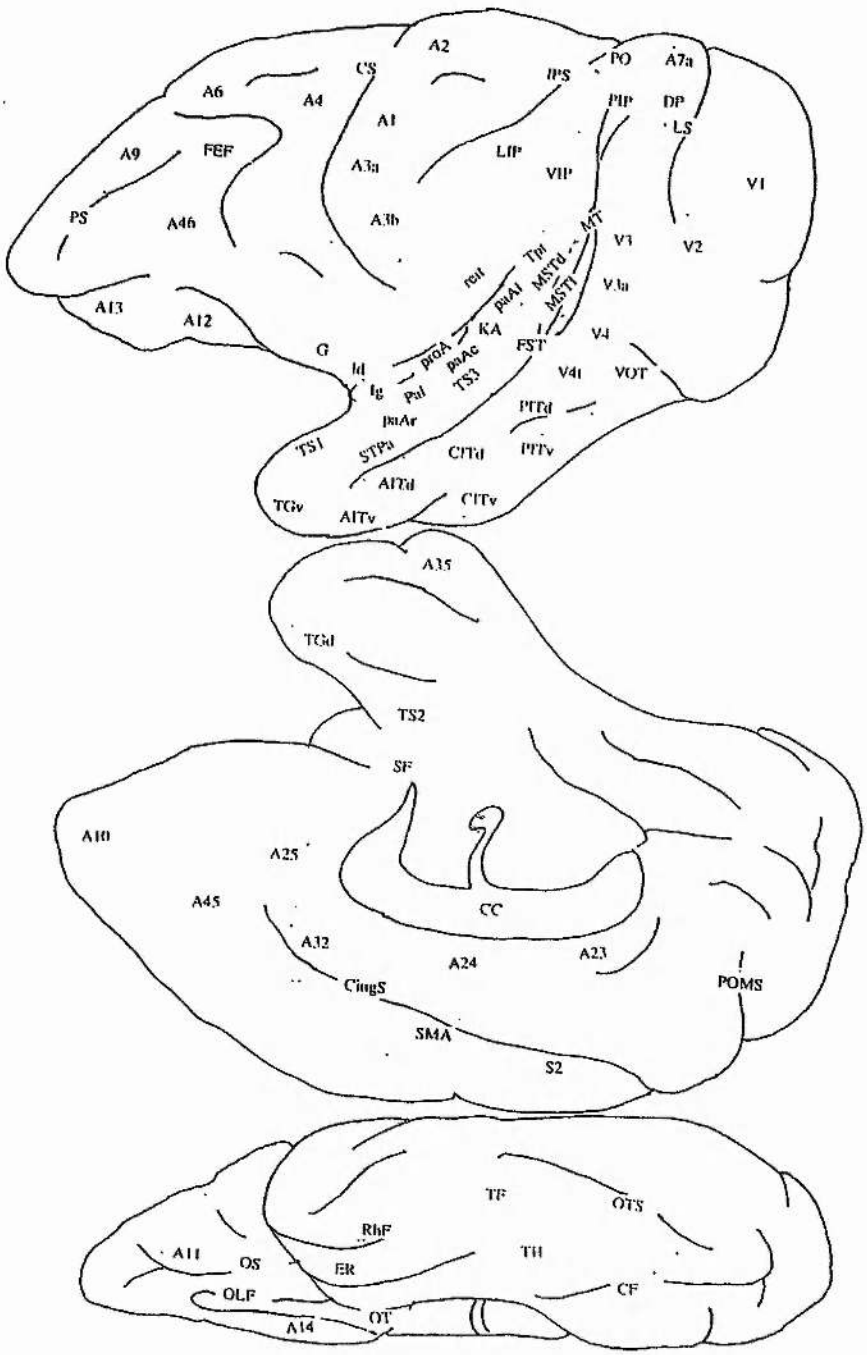
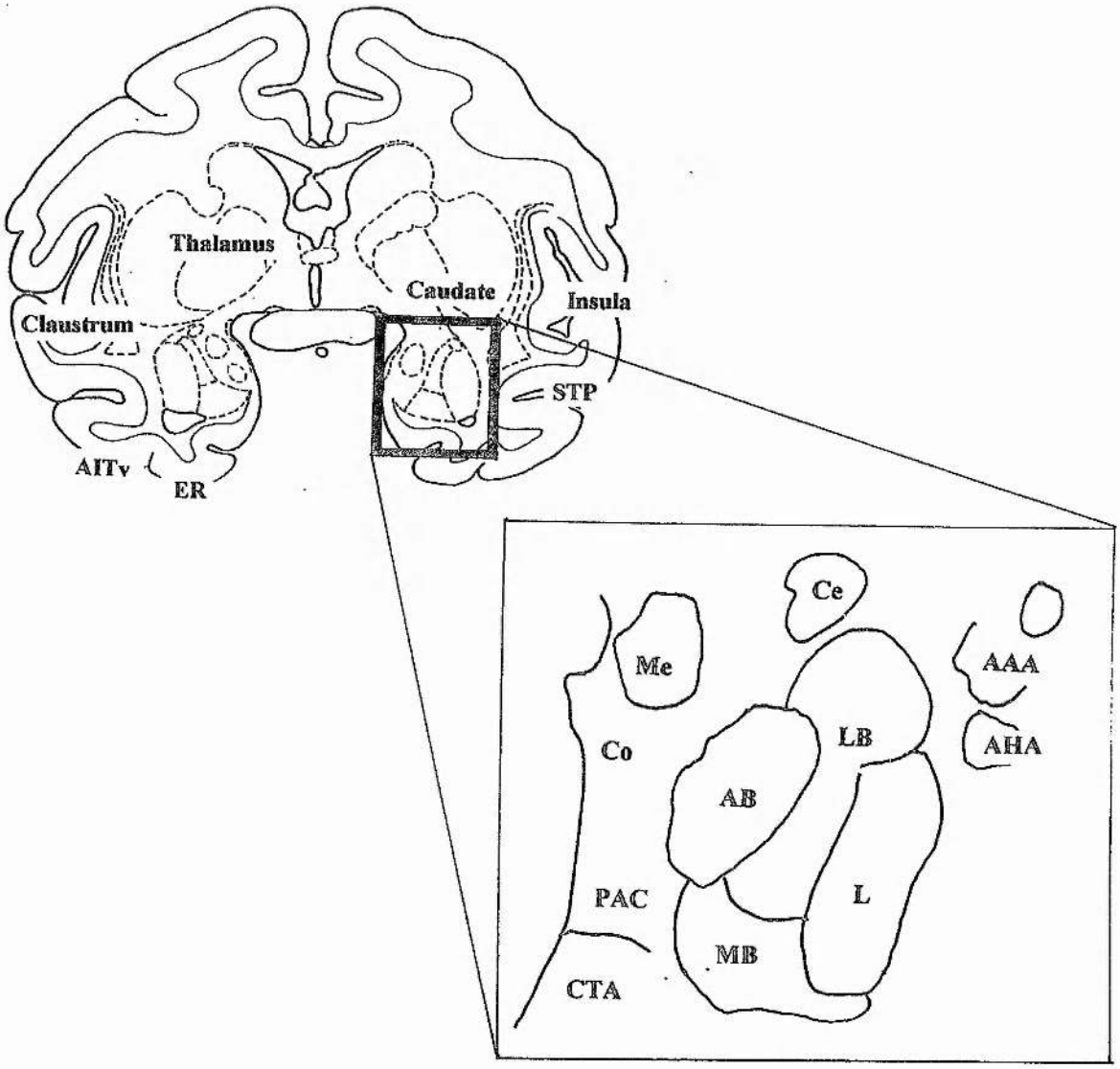


Figure 4.3: (a) Lateral view of the rhesus macaque brain, showing parcellation of cortical areas with abbreviations from Young (1993). (b) Medial view of the macaque brain, with labels as in (a). (c) Ventral view of the macaque brain, with labels as in (a). (d) Coronal section of the amygdala in relation to the STS, and idealised positions of the individual amygdala nuclei, with abbreviations from Amaral et al (1992).




Thalamus
Caudate
Insula
Claustrum
STP
AITv
ER
Ce
Me
AAA
LB
Co
AHA
AB
PAC
L
MB
CTA

4.2.2 Database construction.

An anatomical database was compiled from 42 published papers (1945-1993) of amygdalo-cortical and cortico-cortical connections in the macaque monkey brain and is reproduced in Appendix 1. A connection was included in the database if it was reported in more than one paper (not if the technique used in both papers were neurodegenerative lesions), and the connection was relatively strong, particularly with ten or more (stained/degenerated) cells reported. The database itself contained the directional nature of the connection (unidirectional, or reciprocal), the species of macaque investigated, the number of animals used, the location of the injection site, and final destination of the connection, the anatomical method employed and (if applicable) the density of the connection. These anatomical data were derived from studies of various macaque species (*Macaca mulatta, M. fascicularis, M. fuscata and M. Nemestrina*). Anatomical data from other primate species were not considered here.

The cortico-cortical connections were taken primarily from Young (1993), but also from the following papers (Barnes and Pandya 1992, Cavada and Goldman-Rakic 1989a, b, Felleman and Van Essen 1991, Friedman et al 1986, Galaburda and Pandya 1983, Iwai and Yukie 1988, Markowitsch et al 1985, Morel and Bullier 1990, Pandya and Yeterian 1985, Seltzer and Pandya 1978, 1989b, 1994).

The data used in the database was found from studies using different neuroanatomical research techniques. For example, the neuronal degeneration method used in the 1950's could have reported connections which appeared due to the imprecise nature of the lesion technique, e.g. the lesion damaging an area next to the target lesion area. The majority of the cases reported here are of connections which have been reported in more than one journal article by different authors, and use modern neuroanatomical research techniques, such as horseradish peroxidase (HRP). Earlier studies relied on the degeneration technique, but the results of these studies were added when they had been replicated using more modern techniques.

4.2.3 Connectional matrix

Following methods of Young (1992, 1993), the connection data from the anatomical database were then formulated in a connection matrix. The connections between two structures were assigned a number depending on the presence or absence of a connection between two areas. If a connection did not exist or was not reported in the literature it was given a 0 value in the matrix. If a connection was reported but was apparently unidirectional, it was given a 1 value in the matrix. If the connection was reciprocal between two areas, it was given a 2 value. No information of the cortical laminar destination, strength of connection or direction of projection was attributed to this connection data. This basic data does not contain information on whether the two areas that are connected are proximal or distant from one another in physical distance in the brain.

The ordering of the brain areas along the side of the matrix was determined, for convenience, by grouping sensory, motor, association and amygdala areas together. The ordering of the brain regions in the matrix was randomised, to determine that this did not affect the outcome of the NMDS analysis, and this was found to be the case when the matrix was analysed (see below). The lower triangular half of the matrix is displayed in Figure 4.4, and shows all the connections between the amygdalar nuclei and all the cortical areas (sensory, motor, hippocampal, cingulate and prefrontal). A list of abbreviations is also displayed in Figure 4.4.

4.2.4 Non-metric multidimensional scaling analysis

(a) Untransformed data

Non-metric multidimensional scaling (Young 1970) was performed on the data, using the ALSCAL command language in SPSS for Windows (Young and Harris 1993). NMDS is a data analytic technique which displays a representation of the relative proximities between points. The data utilised here are the presence or absence of a connection between two brain regions. NMDS determines the relationship between two

Figure 4.4: Matrix of the cortical and inter-nuclear connections of the macaque amygdala. The absence or presence of a connection is represented numerically in the matrix. An absence of connection is designated by a '0' in the matrix, a unidirectional connection by a '1' in the matrix, and a reciprocal connection by a '2' in the matrix.

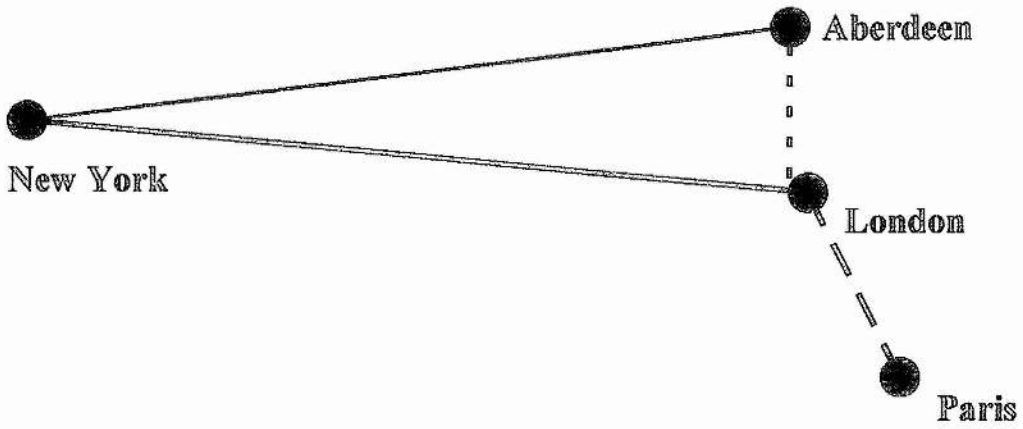
Abbreviations: Anterior amygdaloid area (AAA), Accessory basal nucleus (AB), Amygdalo-hippocampal area (AHA), Dorsal anterior inferotemporal cortex (AITd), Ventral anterior inferotemporal cortex (AITv), Sensorimotor area 1 (A1), Sensorimotor area 2 (A2), Sensorimotor area 3a (A3a), Sensorimotor area 3b (A3b), Primary motor cortex (A4), Somatosensory area 5 (A5), Premotor cortex (A6), Posterior parietal area (A7a), Parietal area 7b (A7b), Dorsal prefrontal cortex (A9), Frontal pole (A10), Rostral orbital frontal cortex (A11), Lateral orbital frontal cortex (A12), Central orbital frontal cortex (A13), Medial orbital frontal cortex (A14), Cingulate gyrus, posterior (A23), Cingulate gyrus, anterior (A24), Medial prefrontal cortex (A25), Prefrontal motor area (A30), Cingulate gyrus, rostral (infralimbic cortex-A32), Perirhinal cortex (A35), Prefrontal cortex, area 45 (A45), Frontal cortex , principal sulcus (A46), Central nucleus (Ce), Dorsal caudal inferotemporal cortex (CITd), Ventral caudal inferotemporal cortex (CITv), Cortical nucleus (Co), Cortical Transition Area (CTA), Dorsal prelunate (DP), Entorhinal Cortex, A28 (ER), Frontal Eye Field, A8 (FEF), Floor of the superior temporal cortex (FST), Gustatory Cortex (G), Hippocampal formation (including the hippocampus and subicular cortices-Hipp), Insular cortex, dysgranular layer (Id), Insular cortex , granular layer (Ig), Primary auditory cortex (KA), Lateral nucleus (L), Lateral basal nucleus (LB), Lateral intraparietal area (LIP), Medial basal nucleus (MB), Medial nucleus (Me), Dorsal medial superior temporal cortex (MSTd), Lateral medial superior temporal cortex (MSTl), Middle temporal area (MT), Caudal parakaniocortical auditory area (paAc), Lateral parakaniocortical auditory area (paAl), Rostral parakaniocortical auditory area (paAr), Periamygdaloid cortex (PAC), Parainsula cortex (PaI), Posterior intraparietal area (PIP), Dorsal posterior inferotemporal cortex (PITd), Ventral posterior inferotemporal cortex (PITv), Prokaniocortical auditory area (proA), Parieto-occipital area (PO), Circular sulcus, area relt (reit), Retroinsular area (RI), Somatosensory area 2 (S2), Supplementary motor area (SMA), Anterior superior temporal polysensory area (STPa), Posterior superior temporal polysensory area (STPp), Parahippocampal gyrus (TF), Dorsal temporal pole (TGd), Ventral temporal pole (Tgv), Parahippocampal gyrus (TH), Auditory area Tpt (Tpt), Auditory area in rostral portion of superior temporal gyrus (TS1), Auditory area in mid-portion of STG and adjacent cortex in superior temporal sulcus (TS2), Auditory area within caudal part of STG and adjacent cortex in STS (TS3), Primary visual cortex , A17 (V1), Secondary visual cortex , A18 (V2), Tertiary visual cortex , A19 (V3), Tertiary visual cortex, a (V3a), Visual area 4 (V4), Visual area 4, transitional (V4t), Ventral intraparietal area (VIP), Ventral occipitotemporal visual area (VOT).

regions by using the similarity of connection patterns between these two brain regions. This is analogous to the possible connections between airports (see Figure 4.5). New York JFK and London Heathrow are physically far apart, but the number of connections (flights) between them are many. The physical distance between London and Aberdeen is much less than the distance between London and New York, but the number of flights between London and Aberdeen is far fewer than between London and New York. In a NMDS analysis of flight connections, London and New York would be close together in the topological plot, and London and Aberdeen would be far apart. Places physically close together can also be topologically close. London and Paris are relatively close and also have a large number of connections between them. The brain also contains regions which are physically close, but poorly connected, and regions which are physically distant, but well connected. The brain also has regions similar to London and Paris in this above analogy, which are physically and well connected.

Distance data is not included in this analysis of brain regions. Two regions are deemed to be proximal to one another if their connectivity patterns are similar, e.g. area X connects to areas Y, Z, A, B, C & D and area Z connects to areas X, Y, A, B, C & E. Areas X and Z have five connections in common. Areas X and Z, therefore, have very similar connection patterns and so would be placed close together in the NMDS output configuration. By contrast, area W connects to areas C, D, G, H, I, & J and therefore does not have a similar connection pattern to areas X and Z. Area W would be placed further away from area X and Z in the output NMDS configuration.

To visualise the output configuration, the NMDS analysis needs to be performed in two or three dimensions, to aid interpretation. The configuration of results is displayed in two dimensions here. Calculating distance in a low number of dimensions mean that not all the important aspects of the matrix data structure may be visualised.

The details of the NMDS procedure are discussed fully in Young, Scannell et al (1995). The model used in the analysis here was similarity distance and the output configuration was plotted in Euclidean square space to aid visualisation (Shepard 1962). NMDS is used to reduce the number of dimensions of the output configuration. Convergence was set to zero, so that SSTRESS was minimised as well as possible. RSQ



Densely connected, positionally close

Loosely connected, positionally close

Densely connected, positionally far

Loosely connected, positionally far

Figure 4.5: Diagrammatic representation of connectional problems solved by NMDS. New York JFK and London Heathrow airports are distant from one another, but the connections between them are many (large number of flights). In similar ways in the brain, two areas may be densely connected, but anatomically distant. London Heathrow and Aberdeen on the other hand, are loosely connected, but positionally close. Paris and London Heathrow are positionally close with a large number of flights between them. Finally, Aberdeen and New York JFK are positionally far and connectionally unrelated.

(simple squared correlation coefficient) and stress values were also computed to determine the level of goodness-of-fit between the computed data and the output configuration. A high RSQ (towards 1.0) indicates the fit is very good and that 100% of the variance between the computed data and the resultant topological plot is explained. A low RSQ (towards 0) indicates that the fit of the data is bad, and that a low amount of the possible variance is explained. A bad fit signifies that the data is not well visualised in a low number of dimensions (2 or 3), or is otherwise a poor representation of the data.

The output topological configuration plots were created by the ALSCAL programme, and lines representing connections between two areas were drawn using custom drawing software.

(b) WDSM1 data transformation method.

In an untransformed matrix, all values are treated with equal weighting, e.g. a zero entry is considered as important as a non-zero entry. To offset the influence of this, the wdsm1 transform (weighted dissimilarity transform-Young, Scannell et al 1995), maximises the importance of the known amygdalo-cortical and cortico-cortical connections (1 or 2 data points) and reduces the importance of the large number of non-reported connections (0 data points). This is achieved by using a formula to convert the 0, 1, 2 data to a meaningful set of values in the matrix. The wdsm1 transform method and formula is described in extensive detail in Young, Scannell et al (1995). The wdsm1 transform treats each connection in the matrix in terms of its own and its nearest neighbour's connectivity patterns. For example, Area X and Area Y have the following hypothetical connectivity patterns, as shown in Figure 4.6.

Area X and Area Y therefore have very similar connectivity patterns and so would be located in similar positions in a basic (non-transformed) NMDS analysis. The wdsm1 transform attempts to reduce the possible influence of the high number of zero entities in the connection pattern of Area Y, by transforming the data in the following way. An element is described as a connection in the matrix (i.e. 0, 1, 2). There is a unidirectional connection (1) between Area X and Area Y. This element in the new wdsm1 matrix is the sum of all the non-zero elements in the Area X row minus the sum

	Y	Z	Q
	0	*1*	*2*
	0	*0*	*0*
	0	*1*	*1*
	0	*1*	*0*
V	*1*	*1*	*1*	*2*	*0*	*2*	***1***	*2*	*2*	*2*	*1*	*1*	*0*	*0*	*1*	*2*
W	*0*	*0*	*1*	*1*	*2*	*0*	*2*	*2*	*1*	*2*	*0*	*0*	*0*	*1*	*0*	
X	***0***	***0***	***0***	***1***	***1***	***2***	***1***	*1*	*1*	*2*	*2*	*0*	*2*	*0*	*0*	*2*
	0	*0*	*0*													
	0	*0*	*1*													
	2	*2*	*0*													
	2	*1*	*1*													
	0	*0*	*0*													
	2	*1*	*1*													
	0	*1*	*2*													

Figure 4.6: Hypothetical connection matrix between brain areas V, W, X, Y, Z, Q. The numbers (0, 1, 2) correspond to those used in the amygdalo-cortical matrix used in this analysis. The numbers in bold italics are the connections of Area X and Area Y, and the number in bold is the connection (matrix element) between Area X and Area Y.

of all the non-zero elements in Area Y. This value is then divided by the sum of all the non-zero elements in the Area X row plus all the non-zero elements in the Area Y row (using the formula below).

$$\textbf{Weighting of new element} = [\Sigma|(\text{Area X}_{me} - \text{Area Y}_{me})|] / [\Sigma|(\text{Area X}_{me} + \text{Area Y}_{me})|]$$

where me = matrix element

Transformed matrix element X/Y would therefore be calculated so. The non-zero numbers in Row X are added together (=15). The non-zero numbers are summed in Row Y (=11). These numbers are then placed into the equation above.

Weighting of new Me = $\Sigma | (15 - 11) | / \Sigma | (15 + 11) | = 4/26 = 0.1538$

Each new element is computed by taking the weighting of the new matrix element from the existing matrix element. In the above example, the old matrix element X/Y was 1. The new matrix element would be 1 - 0.1538 = 0.8462. (NB. the new elements are all "real" numbers). The transformed matrix is then analysed using NMDS in the same way.

4.2.5 Cluster analysis (CA)

Hierarchical cluster analysis (CA) was also performed on the data matrix using the PROXIMITIES language of SPSS for Windows (Norusia 1993). Cluster analysis is a second statistical procedure which groups data points together which have similar properties. Where NMDS groups areas together in a plot (of a multiple possible number of dimensions), CA also groups areas together but determines the relationships between those areas by producing an output dendrogram. The dendrogram visualises the

relationships by representing them as connections on a tree structure (as is commonly used in phylogenetic studies). For example, bonobos and common chimpanzees are closely related. Both species are closely related to gorillas, and bonobos, chimpanzees and gorillas are related to orangutans (see Figure 4.7 below). CA can also be used to determine the precise relationships between areas using their connection patterns. CA was performed on the raw, untransformed data. .

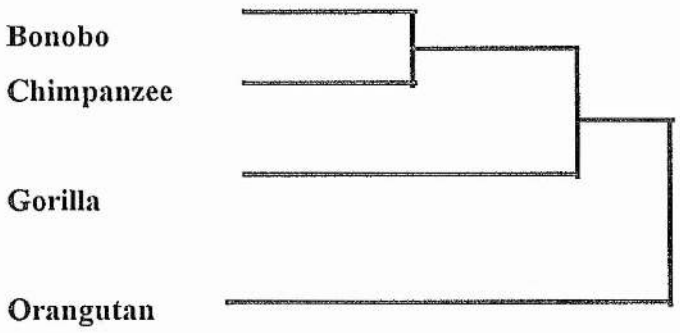


Figure 4.7: Dendrogram displaying the genetic (evolutionary) relationship between species of great apes. Bonobos and chimpanzees are most closely related, so are connected together; gorillas are related to both these species, and orangutans are related to all of them.

4.2.6 Connectional Density Index (CDI)

Each area in the matrix can connect (unidirectionally or reciprocally) with a possible 83 other areas (including intra-areal connections). A *Connectional Density Index* (CDI) was computed for each brain area. CDI's were computed as indicators of the density of connections of each area out of the total possible number of connections for that area. For example, area X may have 72 out of a possible 83 connections, whereas area Y may only have 34 out of a possible 83 connections. Area X would have a

relatively high CDI and area Y would have a relatively low CDI. CDI was calculated as follows:

CDI = Area X, total no. connections (unidirectional or reciprocal) / 83

where 83 is the total possible number of connections in the matrix.

4.3 Results

The anatomical database, contained 951 reported connections, with 503 reciprocal connections (52.9%) and 448 unidirectional connections (47.1%). There were 83 structures in the database, so there were 3445 possible connections between all areas, (including intra-areal connections), so the 951 reported connections were 27.6% of the total possible connections. The matrix therefore contained a large number of non-reported connections. The 83 areas reported were classified into categories; visual, auditory, somatosensory, motor, cingulate cortex, hippocampal areas (hippocampus, entorhinal and perirhinal cortices) and prefrontal cortex. The parcellation of each sensory/motor/association cortical area or amygdala nucleus is described in the legend to Table 4.1. The number of areas in each category (based on the physiological properties of single neurons in these areas, and/or their architectonic boundaries), is shown in Table 4.1. Table 4.1 also displays the number of connections that each group (sensory, motor, association or amygdala) has reported in the matrix and an index of connectivity for each group dependent on the number of brain areas within a group. There are many visual areas and these areas have many connections. The amygdala has many connections from a relatively small number of areas, whereas the hippocampal areas have many connections from a few areas.

Table 4.1 shows that the hiipocampal formation has a large number of connections relative to the number of brain areas (13.7). The amygdala (10.4) and the prefrontal cortex (5.5) also have relatively large numbers of connections relative to number of brain areas. The primary sensory and motor groups (visual, auditory,

Table 4.1: The number of brain areas that contribute to a particular modality or functional group, and the percentage number of total areas in the amygdala connections database. The number of connections with each group (matrix entries) and the percentage number of total connections are also displayed. Each score is ranked (1-8, 1=highest number of areas/connections, 8=lowest number of areas/connections). The number of connections, dependent on the number of areas (i.e. number of connections/number of areas) are also displayed, with rank. Groupings; visual (V1, V2, V3, V3a, V4, V4t, VOT, VIP, LIP, PIP, DP, PO, AITd, AITv, CITd, CITv, PITd, PITv, FEF, FST, MT, MSTl, MSTd, STPa, STPp, TF, TH, TGv, A7a, A46), auditory (KA, PaI, paAl, paAc, paAr, proA, reit, TGd, Tpt, TS1, TS2, TS3), somatosensory (Id, Ig, S2, A1, A2, A3a, A3b, A5, A7b, RI), motor (A4, A6, SMA, A30), cingulate (A23, A24, A32), hippocampal (Hipp, A35, ER), prefrontal (A9, A10, A11, A12, A13, A14, A45, A25, G), amygdala (L, LB, AB, MB, Co, Ce, AAA, AHA, CTA, Me, PAC).

Group	**No. of Areas (A)**	**% Total (A)**	**Rank (A)**	**No. of Connections (C)**	**% Total (C)**	**Rank (C)**	**C/A**	**Rank (C/A)**
Visual	30	36.2	1	109	26.5	2	3.6	5
Auditory	12	14.5	2	32	7.8	6	2.7	7
Somatosensory	10	12	4	45	10.9	4	4.5	4
Motor	4	4.8	6	4	1.0	8	1	8
Cingulate	3	3.6	7	11	2.7	7	3.6	5
Hippocampal	3	3.6	7	41	10.0	5	13.7	1
Prefrontal	10	12	4	55	13.4	3	5.5	3
Amygdala	11	13.3	3	114	27.7	1	10.4	2
Total	**83**	**100**		**411**	**100**			

somatosensory and motor) have few connections relative to the number of areas within each group.

The number of connections (efferent and afferent) of the individual amygdala nuclei are displayed in Table 4.2. The LB nucleus has the largest number of total connections, with the greatest number being efferent and afferent connections with visual areas (particularly with the temporal cortical areas). The L nucleus has multiple connections with the ventral visual cortical areas of the temporal lobe. Other areas which are prolifically connected to parts of the amygdala are the prefrontal cortical areas with the LB, MB and AB nuclei, and the somatosensory and auditory areas with the AB nucleus.

The largest number of input and output connections of the various cortical areas is with the BL group of amygdala nuclei. The number of input or afferent connections are far outnumbered by the number of output or efferent connections for the majority of the amygdala nuclei. This differs for the L nucleus, which receives the largest number of its connections, but outputs relatively few to the cortex (with the exception of the ventral visual areas). The L nucleus does project to every other amygdala nucleus, but receives very sparse return connections from these nuclei.

4.3.1 Non-metric multidimensional scaling analysis.

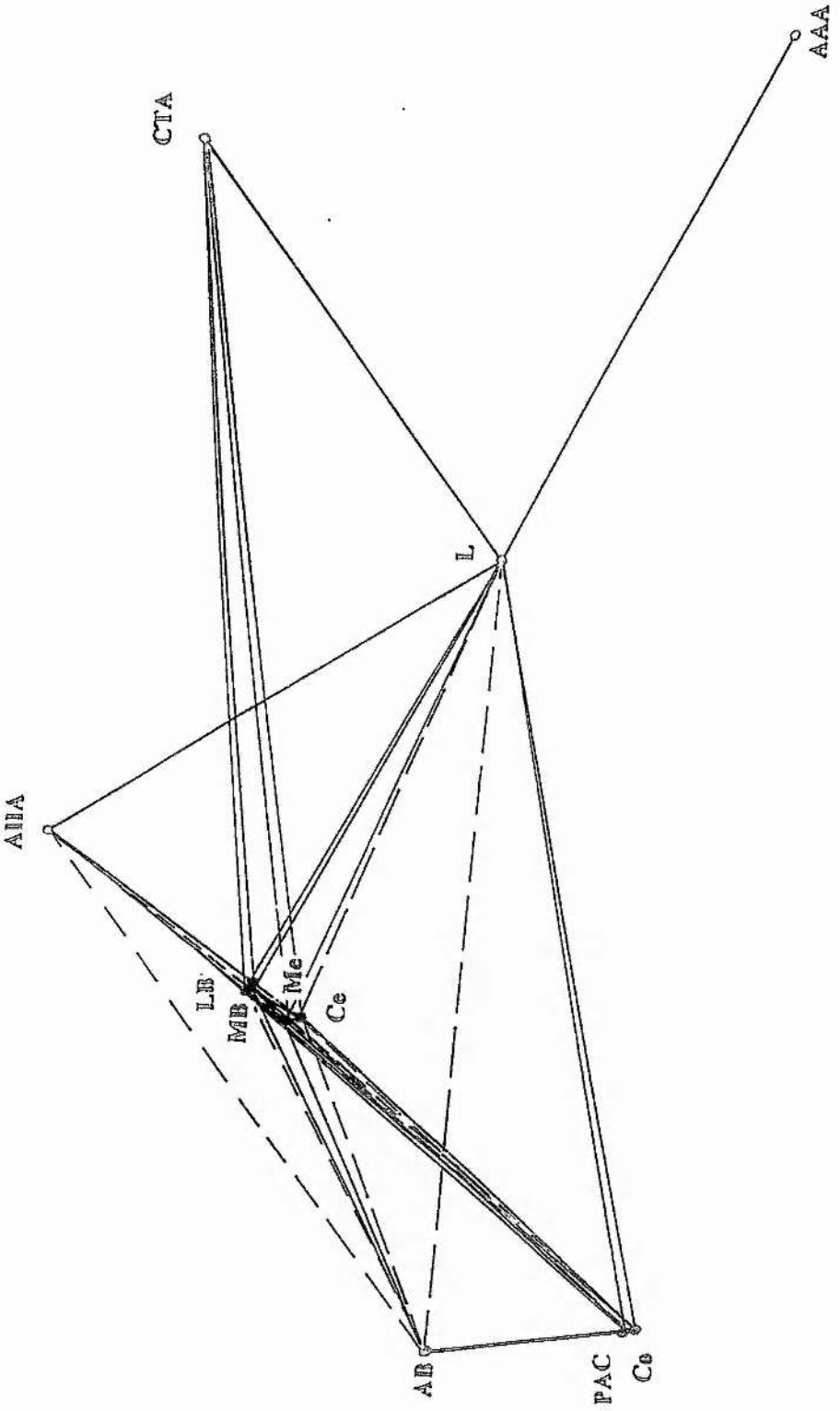
(a) Intra-amygdala connections

The intrinsic connections of the primate amygdala were analysed with NMDS using a basic matrix (0, 1, 2) without transformation of the data, and the resulting 2D configuration of data points is displayed in Figure 4.8. The RSQ value of the output configuration plot was 0.645, so 65% of the relations in 83 dimensional space were accounted for. (NMDS computed the relations between brain areas in 83 dimensions, but the resulting configuration could not be visualised in 83 dimensions, so some relationships would be lost by visualising in 2D. There would be less loss of relations in 3D, etc.)

Table 4.2: Number of efferent and afferent connections of each amygdala nucleus with each sensory/motor/associative group. Cortical grouping the same as Table 4.1. Eff = efferent connections, Aff = afferent connection. The amygdala abbreviations are the same as in Figure 4.4.

Amygdala Nuclei	Visual		Auditory		Somatosensory		Motor		Hippocampal		Prefrontal		Cingulate		Cortical Total		Amygdala		TOTAL		
	Eff.	Aff.	Eff.	Aff.	Eff.	Aff.	Eff.	Aff.	Eff.	Aff.	Eff.	Aft.	Eff.	Aff.	Eff	Aff.	Eff	Aff	Eff.	Aff.	Total
L	11	12	2	4	2	2	1	0	3	1	3	4	0	1	22	24	13	2	35	26	61
LB	24	10	2	1	3	2	2	0	3	0	10	5	2	1	46	19	8	6	54	25	79
MB	10	4	1	0	3	2	1	0	3	3	9	2	2	0	29	11	8	4	37	15	52
AB	11	5	8	1	9	2	0	0	3	2	7	2	3	0	41	12	6	6	47	18	65
Ce	1	5	1	2	2	2	0	0	3	3	0	2	0	0	7	14	9	5	16	19	35
Co	3	1	1	1	2	1	0	0	3	2	4	0	1	0	14	5	2	7	16	12	28
Me	1	4	1	1	1	1	0	0	2	1	0	5	0	1	5	13	7	4	12	17	29
PAC	4	1	3	1	8	0	0	0	1	2	1	0	0	0	17	4	5	6	22	10	32
AAA	1	0	1	0	1	2	0	0	0	1	1	0	0	0	4	3	0	2	4	5	9
AHA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	6	3	6	9
CTA	1	0	1	0	0	0	0	0	1	1	0	0	0	0	3	1	0	5	3	6	9
Total	67	42	21	11	31	14	4	0	22	16	35	20	8	3	188	106	61	53	249	159	408

Figure 4.8 : The topological organisation of the internal connections of the primate amygdala, as visualised using NMDS, basic transformation. From a total of 42 connections, 28 are unidirectional (line) and 14 are reciprocal (broken line). Abbreviations as in legend to Figure 4.4.



The L nucleus lies at the centre of the plot, the LB, MB, Me and Ce nuclei are grouped together, and the remaining nuclei (Co, PAC, AAA, AHA) are collected on the outside edges of the topological plot, distant from the other nuclei. It is interesting to note here that the Co nucleus and PAC are grouped together. The connections of these two areas are probably similar due to their close physical proximity.

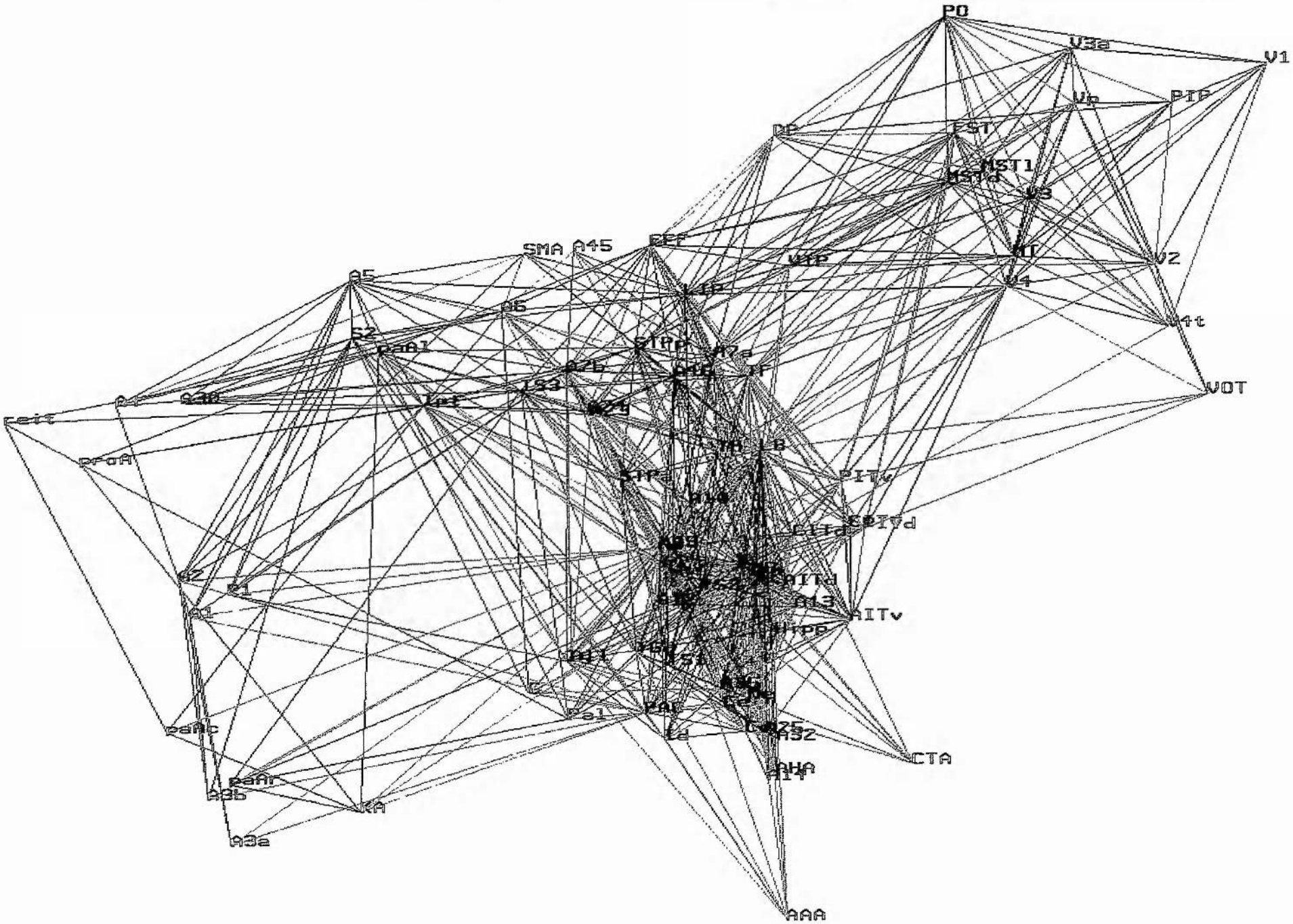
(b) Amygdalo-cortical connections

The amygdalo-cortical connections of the monkey cortex were analysed using NMDS (using the ALSCAL command language in SPSS). In this analysis, a total of 951 connections, 503 (52.9%) were reciprocal, and 448 (47.1%) were unidirectional. The resulting analysis had a RSQ value of 0.76, therefore the topological relations expressed in the 2D solution, accounted for 76% of the relations covered in the original 83 dimensional space.

The NMDS analysis plot is displayed in Figure 4.9. The very distinct separation of the BL and CM amygdaloid complexes is of primary interest here. The CM complex is placed with the prefrontal cortical areas in Figure 4.9 and is completely separate from the BL amygdala nuclei. As the CM nuclei are grouped with the prefrontal cortical areas and there is a strong interconnectivity between the nuclei within the BL and CM complexes (as seen in the intra-amygdala analysis); a possible flow of information between the BL complex and the prefrontal cortex may be via the CM nuclei of the amygdala. The LB nucleus is proximal to both visual processing streams, but is pulled away from the BL complex towards the dorsal visual areas. The MB and L nuclei are close to the ventral visual processing areas of the inferotemporal cortex (PIT, CIT and AIT). The hippocampal formation, perirhinal and entorhinal cortices are located between the CM and BL groups. The periamygdaloid complex (PAC) is located close to the CM group and may warrant its inclusion in the CM group. The peripheral amygdala nuclei (AHA, AAA and CTA) remain clearly separate from the other amygdala nuclei, which may be due principally to their low number of cortical connections.

From the figure, it can be seen that the auditory system areas within the superior temporal gyrus are grouped in similar locations on the plot, with connections between

Figure 4.9: The topological organisation of the amygdalo-cortical system, as visualised by NMDS, and transforming the data matrix using the wdsm1 transform formula. From a total of 951 connections, 448 are unidirectional (green) and 503 are reciprocal (red). Abbreviations as in legend to Figure 4.4.


PO
V3a
V1
Vp
PIP
DP
FST
MSTl
MSTd
V3
V2
V4
V4t
VOT
PITv
CPITd
AITd
AITv
HIPP
CTA
AAA
SMA
A45
PEF
VIP
A5
A6
A7a
A7b
A46
A9
A8
A32
A13
A3a
A3b

primary auditory cortex (KA) and secondary (association) auditory cortical areas. The auditory areas connect with the AB nucleus of the amygdala and the AB nucleus lies close to the auditory areas in the plot. Figure 4.9 also shows the grouping of somatosensory areas; primary somatosensory areas (A1 and A2), the insula areas (Ig and Id), A3a and A3b, A5 and S2. The motor areas are also located in similar spatial locations, positioned closely to the dorsal visual areas, particularly the FEF (which has oculomotor functions as well as visual functions-Leichnetz and Goldberg 1988).

The visual areas are also collected together in Figure 4.9, with the "dorsal visual areas" of the dorsal occipital and parietal lobes grouped together, and the "ventral visual areas" of the ventral occipital and inferior temporal lobes grouped together. No information about direction of flow is present in Figure 4.9, but the results seem compatible with the idea of two visual processing streams (Ungerleider and Mishkin 1982, Goodale and Milner 1992, Young 1992, 1993). Adding the amygdala as constituent parts into the analysis does not appear to alter the positions of the two visual processing streams.

Evident in Figure 4.9 is the pulling in of "higher order" sensory and motor areas (such as STPa, A46, paAl, paAc, paAr, Ig and Id) towards the central position of the topological plot, with the BL and CM amygdala groups, and the prefrontal cortex. This is not the case for all sensory and motor association areas, but a trend is displayed.

4.3.2 Cluster analysis

The output dendrogram from the cluster analysis is displayed in Figure 4.10. As with the NMDS analysis, the amygdala is split into three parts; the BL complex (LB, L, MB and AB), the CM complex (Ce, Co, Me and PAC) and the peripheral nuclei (CTA, AAA, AHA). In the BL complex, the MB and AB are closely related, with the L nucleus related to both the AB and MB nuclei and the LB linked to all three. This suggests that the connection patterns of the AB and MB nuclei are similar, with the L nucleus close connectionally but distinct, and the LB nucleus strongly associated with the L, MB and AB nuclei, but its large number of connections with other brain regions force its position away slightly from the other nuclei in the BL complex.

Figure 4.10: Dendrogram displaying results of cluster analysis of amygdalo-cortical connections. The abbreviations of cortical and amygdala areas are the same as in the legend to Figure 4.4. The BL group of nuclei is grouped together, as is the CM group and the peripheral nuclei.

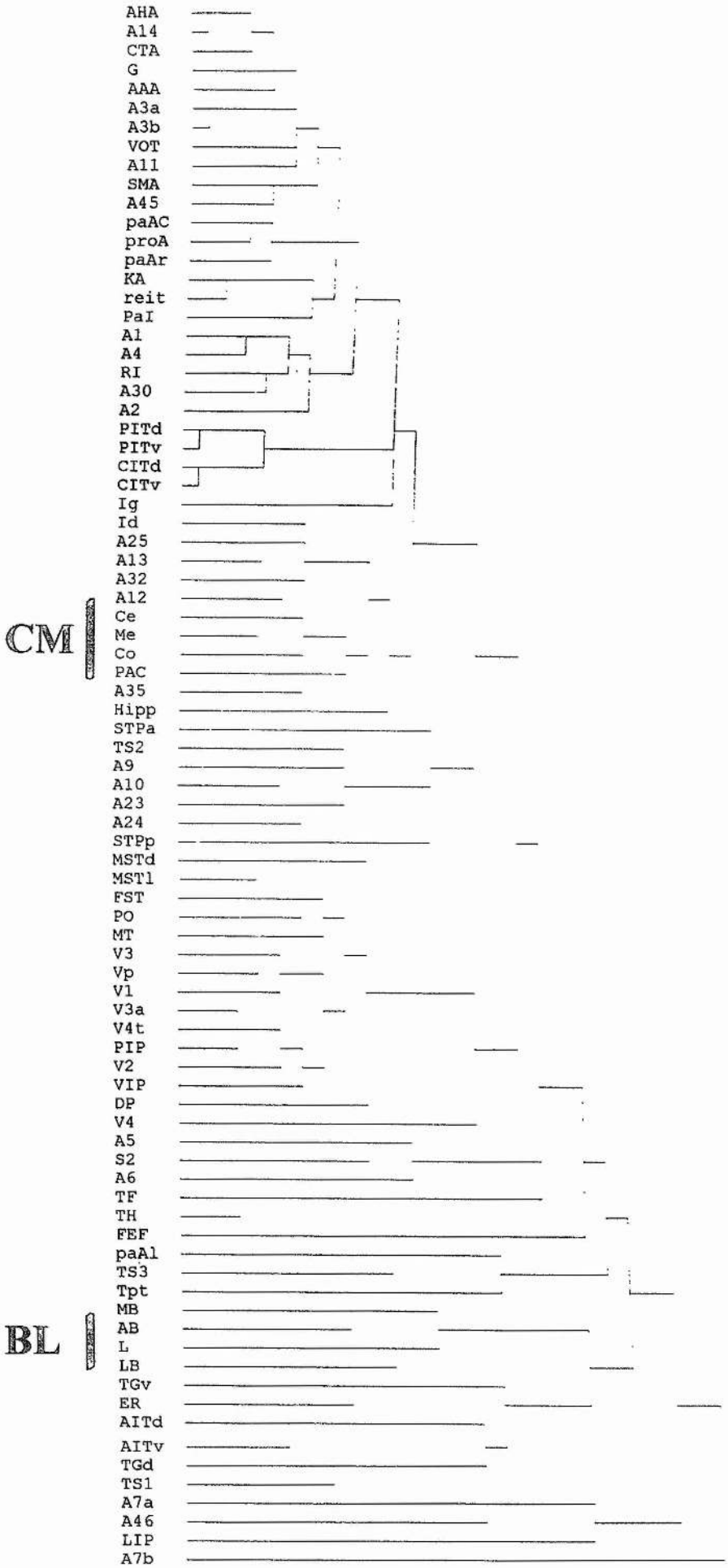
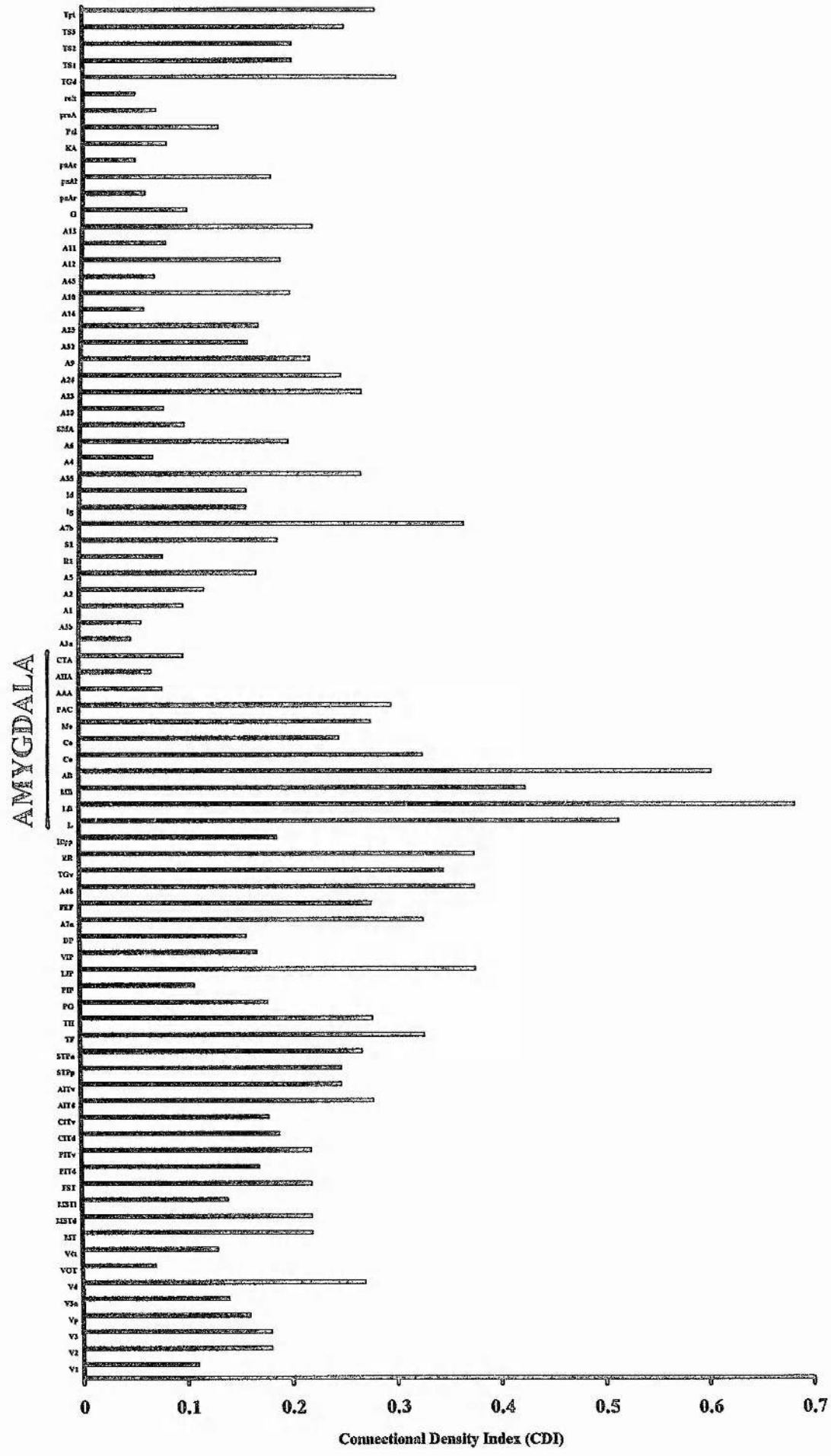

AHA
A14
CTA
G
AAA
A3a
A3b
VOT
A11
SMA
A45
paAC
proA
paAr
KA
reit
PaI
Al
A4
RI
A30
A2
PITd
PITv
CITd
CITv
Ig
Id
A25
A13
A32
A12
Ce
Me
Co
PAC
A35
Hipp
STPa
TS2
A9
A10
A23
A24
STPp
MSTd
MSTl
FST
PO
MT
V3
Vp
Vl
V3a
V4t
PIP
V2
VIP
DP
V4
A5
S2
A6
TF
TH
FEF
paAl
TS3
Tpt
MB
AB
L
LB
TGv
ER
AITd
AITv
TGd
TS1
A7a
A46
LIP
A7b
CM
BL

Figure 4.11: Diagrammatic representation of the Connectional Density Index (CDI) values for each area in the matrix (out of a total of 83). The y-axis shows the brain areas (abbreviations the same as in the legend of Figure 4.4). The x-axis shows the individual CDI scores.


AMYGDALA
Tpt
TS5
TS2
TS1
TGd
rs2
proA
Pd
KA
proAc
proAl
proAr
Cl
A13
A11
A12
A45
A10
A14
A23
A52
A9
A24
A22
A32
SMA
A6
A4
A35
Id
Ig
A7b
SI
Ri
A5
A2
A1
A3b
A3a
CTA
AHA
AAA
PAC
Me
Co
Ce
AB
MB
LB
L
IDpp
ER
TGv
A46
PEF
A7a
DP
VIP
LIP
PIP
PO
TH
TF
STPa
STPp
AITv
AITd
CITv
CITd
PITv
PITd
FST
FSTl
FSTd
ST
Vis
VOT
V4
V3a
Vp
V3
V2
V1
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Connectional Density Index (CDI)

A similar position exists for the CM complex. The Ce and Me nuclei are closely associated; the PAC is closely related to both the Ce and Me nuclei, and the Co nucleus is related to all three, but is also related to areas of cortex (and the BL complex), so is separated slightly from the other components of the CM complex.

4.3.3 Connectional Density Index

A visual representation of the CDI scores for the 83 brain areas is displayed in Figure 4.11. The nuclei of the BL complex of the amygdala have the largest percentage of connections; LB (69%), AB (61%), L (52%) and MB (43%). The nuclei of the CM complex have a relatively lower percentage of connections compared to the nuclei of the BL complex; Ce (33%), PAC (30%), Me (28%) and Co (25%). The only regions of cortex which are as well connected as the CM complex, are the ER (38%), LIP (38%), A46 (38%), A7b (37%), TGv (35%), A7a (33%) and TF (33%). None of the primary sensory/motor areas are well connected with the rest of cortex.

5.4 Discussion

To summarise, the internal connections of the amygdala reveal a strong association between the LB, AB and MB nuclei (or "BL" group) and the Co, Me, and Ce nuclei and the PAC (or "CM" group). The L nucleus lies at the centre of the NMDS plot as it connects to every other amygdala nuclei, and the poorly connected peripheral nuclei (AAA, AHA and CTA) are placed separately on the outside edge of the plot. There is no apparent separation of the BL and CM groups when analysing the internal connections only, as their are reciprocal heavy connections between these two groups. This supports the view that the BL complex receives sensory information, which is then passed onto the CM complex, with high levels of communication between the two groups. The gross structure of the NMDS plot is presented schematically in Figure 4.12.

In the amygdalo-cortical analysis, the sensory and motor areas group together, as do the areas of the hippocampal formation. The amygdala spilts into three parts. The BL

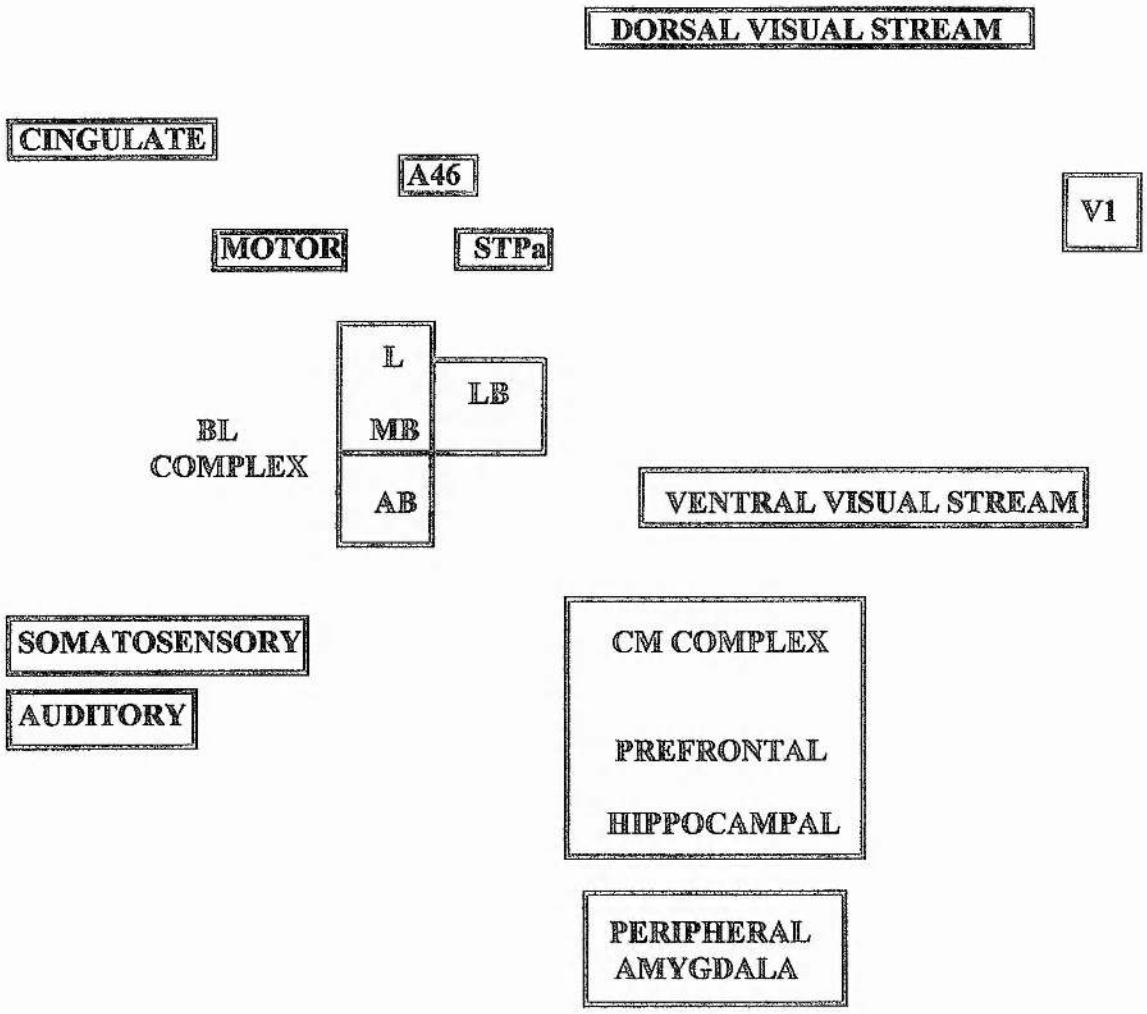


Figure 4.12: Schematic representation of the NMDS output displayed in Figure 4.7. The diagram shows the proximity of the main brain regions to one another. The general collections of areas are based on a large number of areas in a group being aggregated together. The cortical areas of the dorsal and ventral visual processing streams are grouped together, as are the auditory, somatosensory and motor cortical areas. The LB nucleus is distinct from the other BL complex nuclei, and the CM complex nuclei are grouped together with the nuclei of the prefrontal cortex. The peripheral nuclei of the amygdala (AAA, AHA, CTA) are grouped on the periphery of the plot. The hippocampal formation and cingulate cortical areas are also grouped with the anterior temporal area (od the ventral visual stream) and the BL complex.

group is closely associated with the anterior temporal visual processing areas, and to a lesser extent the auditory and somatosensory association areas. The CM group is closely related to the prefrontal cortex, and the peripheral amygdala nuclei lie at the edge of the NMDS plot.

The monkey cerebral cortex is largely parcelled into areas that have similar connectivity patterns (Young 1993) and this was apparent in this analysis. These similarities are striking when the functional aspects of the areas are taken into consideration. It appears that all areas of a cortical sensory processing group (e.g. somatosensory) group together in the NMDS due to their anatomical connections. NMDS may be a useful tool in ascribing similar functions to areas with similar patterns of connectivity. This is displayed distinctively when the whole cortex and amygdala is subjected to NMDS analysis. As stated earlier, physical distances between brain regions were not taken into consideration in this analysis. If two brain regions are close in the topological plot, they are connectionally similar, and visa versa. Physical distance does not constrain topological distance, that is, two brain regions that are physically close together do not necessarily have similar connectivity. For example, the amygdala nuclei AAA and LB, are physically close in the amygdala, but in the topological plot they are distant, and therefore, connectionally dissimilar.

Young (1992), using a matrix of cortico-cortical connections of the visual system, argued that the concept of two "functional processing streams" of the visual system (Goodale and Milner 1992, Ungerleider and Mishkin 1982), was apparent also because of their individual connectivity patterns. The "dorsal" stream travelling from V1 through MT, MST, posterior parietal cortex, through A7a to FEF and A46 in the frontal lobe was present in the plots of the NMDS analysis (Young 1992). The "ventral" stream from V1 through V4, to inferotemporal (IT) areas and STPa to A46 was also present in the same analysis. Young (1992) also argued that the two processing streams could converge in A46 and STPa. This information is present in this analysis, but is not as clear as in Young's (1992) study. The ventral stream could be seen as a route by which visual information (objects such as faces) can be processed further to attribute an emotional or social significance to the observed object. Visual form information increases in

complexity from V1 to V4, IT and TGv. Complex, but emotionally/socially "insignificant" objects, such as fractal patterns and complex geometrical shapes, are processed in inferotemporal cortex and ventral temporal pole (Tanaka 1993, Tanaka et al 1990, Miyashita et al 1993, Nakamura et al 1994). Although such complex patterns and shapes are not in themselves socially/emotionally significant, they could constitute parts of such biologically important visual stimuli. Biologically important objects, such as faces, bodies and hands, are processed in IT and STPa (Bruce et al 1981, Perrett et al 1982, Desimone et al 1984, Wachsmuth et al 1994), which have prolific connections with TGv, TF and TH. Inferotemporal cortex and STPa have many connections between them (see Chapter III) and are closely associated with the "BL" nuclei of the amygdala in this analysis. These connections could allow such complex information to be attached an emotional or social significance. Such visual information could be used by primates to help infer the intentions and predict the behaviours of conspecifics in normal social interactions (Perrett and Emery 1994, see also Chapter VII).

The hierarchical organisation of the primate auditory system has also been tentatively suggested (Felleman and Van Essen 1991, Young 1993). This proposition is not substantiated or refuted by the present study. There is a loose grouping of auditory areas, with the primary auditory areas (KA), grouped next to secondary and tertiary auditory areas (such as paAc and paAr) in the anterior superior temporal gyrus, with the AB nucleus of the amygdala pulled away from the BL group towards the "higher" auditory processing areas. If there is a hierarchical nature to the connectivity of the auditory system, as displayed in the cat cerebral cortex (Scannell and Young 1993), this "pathway" may either be involved in auditory learning and memory, or may be involved in the processing of the social/emotional significance of monkey vocalisations. The amygdala contains cells which respond to different monkey calls, and when the amygdala is stimulated, similar vocalisation patterns are produced (Jurgens 1982). Such cells are found in the BL and CM groups. Areas of the frontal cortex which connect to the amygdala may function in determining the meaning of the various vocalisations or send back information to the amygdala concerning the production of a correct response to the heard vocalisation (Ploog 1981). The AB nucleus connects directly with many auditory

areas, such as TGd (dorsal temporal pole), Tpt, paAc, paAr, TS1 (anterior superior temporal gyrus auditory area) and KA (primary auditory cortex). Auditory information may thus reach the amygdala via primary auditory cortex, secondary/tertiary auditory cortex or higher association auditory cortex routes. Cells in the lateral areas of the macaque auditory cortex (such as paAc and paAr) which connect to the amygdala, also respond preferentially to complex sounds, also differentiating between different monkey calls (Rauschecker et al 1995). It is known that monkeys use different calls to report social information such as the location of a food source, or the presence of a particular type of predator (Seyfarth et al 1980a, b), and such social information may be processed by this system.

Connections between the amygdala and the somatosensory areas maybe routes by which tactile information can be linked to experience with a social or emotional significance. This information could then be passed from the amygdala on to the ventromedial frontal cortex, and premotor/motor cortex and translated into a behavioural/motor action (Fuster 1996). Information of this type would then be passed back to the body/viscera via the actions of the motor system, neuroendocrine system (via the hypothalamus), or via basic motivational or regulatory mechanisms (via the midbrain and brainstem). The information from the motor areas may pass back through the amygdaloid complex, which has extensive connectivity with these subcortical regions, particularly with the CM nuclei.

Friedman et al (1986) have suggested that there is a tactile processing pathway from the primary somatosensory area S2, through the insula (Ig and Id) and on to the amygdala, and that this pathway might serve a function in tactile learning and memory. The topological proximity between the amygdala and somatosensory areas is only evident between the AB nucleus and the somatosesnsory areas A1, A2 and RI, and between the proximity of the CM complex and the insula areas (Ig and Id). The high level of connectivity between the amygdala and the somatosensory cortical areas may arise due to the importance that Old World monkeys and great apes put on grooming in a social context. The amygdala may associate social/emotional significance to a certain somatosensory event. For example, a monkey may be able to recognise the difference

between a playful slap and a slap as an attacking gesture, or the difference between grooming for cleaning and grooming as a form of alliance formation (Byrne and Whiten 1988). Grooming is also said to aid in the maintenance of group cohesion in certain species of non-human primates (Dunbar 1991). The amygdala, as stated previously, also has connections with the multi-modal cortex of the STPa, where collections of cells respond to various social somatosensory stimuli, such as stroking, and grooming (Mistlin and Perrett 1990), particularly allogrooming (unexpected touch), since the cells did not respond to self-grooming (expected touch). This region also contains cells which are responsive to multiple modalities, such as touch and vision, and only respond when both sensations are presented simultaneously. Such cells responding to touch and sight, may code for not only the act of grooming (touch), but also the identity of the grooming animal (sight). Such information is important when forming alliances, and computing the structure of dominance hierarchies (Cheney and Seyfarth 1990c).

Historically, the amygdala has been studied as a component part of the limbic system, a group of cortical and subcortical areas which have basic functions, such as emotion, spatial memory and species-specific behaviours (MacLean 1952). The idea of the limbic system has recently been questioned (LeDoux 1991), but the cortical and amygdala areas of the limbic system analysed here are all groupd quite close together in the topological plot. The BL and CM nucleic groups are associated with the prefrontal/orbitofrontal cortical areas, the "higher" sensory areas (those association areas which code for complex sensory stimuli), the anterior cingulate cortex, and the hippocampal formation. This conclusion parallels that of Young and Scannell (Young 1993, Young and Scannell 1993) who stressed that there is a Fronto-Limbic Complex, connecting the amygdala, hippocampus, entorhinal, perirhinal, cingulate and prefrontal cortices in monkeys. The analyses of Young and Scannell were similar to the analyses performed here, but the amygdala was treated as a unitary structure. Separating the constituent parts of the amygdala did not disturb the view of a Fronto-Limbic Complex. The "higher" sensory areas are topologically closer to each other or the amygdala in the plot, than primary and secondary sensory areas.

There is a high level of connectivity between the amygdala and the neocortex, with similar connection strengths between all sensory/association areas and the amygdala, so the amygdala was placed in the centre of the topological structure in Young and Scannell (1993, see Figure 4.2). Differences in the results of the two analyses are apparent because the amygdala was analysed with separate nuclei with different weights of connections (i.e. the BL group has more cortical connections than the CM group). This resulted in the different nuclei of the amygdala remaining near the centre of the plot, but with clear divisions between the nuclei.

The BL and CM groups appear as two separate entities, as distinctly shown in Figure 4.9. The LB nucleus is associated with the ventral visual cortical areas which are said to play a role in object recognition. The anterior cingulate cortex is also close to the LB nucleus and the hippocampal formation, entorhinal and perirhinal cortices are placed in between the two amygdala groups.

The above discussion is an attempt to formulate a basic theoretical framework of the architecture of those areas of the brain which have functions in some aspects of monkey social cognition and perception. Such theoretical frameworks may be useful, particularly when discussing global theories of brain function. It is easy to be misled by the results of such analyses, especially when considering distinct brain regions as one unit, when they are actually comprised of millions of cells. Single cells have very specific and complex response properties, and extremely diverse and complicated connectivity patterns of their own (Martin 1988). Generalising a function to an area may be a gross over-simplification. The role that other important subcortical areas such as the basal ganglia, hypothalamus, superior colliculus and thalamus may play in social and cognitive processing was not considered in this analysis, and the subcortical connections of the monkey amygdala would need to be analysed to begin to achieve this. Such studies would be important when discussing the role of the CM nuclei, due to their extensive connections with subcortical areas (Amaral et al 1992).

NMDS analysis, while having certain limitations (such as a necessarily simplified view of brain connectivity), does allow development of ideas about how particular regions might be viewed in the brain, not only as single entities, but also as parts of

functionally integrated systems. NMDS also has another possible function, apart from being a statistical tool. As structure is often related to function, NMDS could be used as a tool to direct neurophysiological and lesion studies. Scannell et al (1996) is an example of the use NMDS analysis of the connections of the cat cerebral cortex to guide successful physiological studies. NMDS in this study suggests possible targets for neurophysiological studies of visual social perception, determined due to the similarity of the connectivity patterns of the ventral and medial temporal areas, which are said to code for complex biologically significant objects and actions (Perrett and Emery 1994, Chapter VII). Similar avenues of research may stem from comparable statistical analyses using neuroanatomical data as a starting point for beginning more functional lines of research.

The NMDS and CA analyses suggest that the amygdala can be split into two functional groups; the BL and CM complexes. The BL complex has more numerous connections with cortical areas, including high order sensory processing areas which may be involved in social cognition. The parcellation of the amygdala into two divisions provides a basis for analysis of comparative volumetric data of the two divisions (and constituent parts of the amygdala) in the next chapter (V).

Chapter V

Architecture of the Primate Social Brain

C. Comparative Analysis

"Our knowledge of the evolutionary transformation of hominid social systems is primarily based on comparative studies of primates....If these approaches are to be of value for understanding the behavior and evolution of nonhuman primates or humans...then it must be demonstrated that the bases for complex behaviors are differentially inherited and have evolved"

Armstrong, Clarke and Hill (1987, p. 263)

5.0 Summary

In the previous chapter, the connections of the macaque neocortex and amygdaloid complex were analysed using a statistical method (NMDS) which groups brain areas together with similar connection patterns. It was found that three brain regions said to be the primary components of the so-called "social brain" (basolateral amygdala, anterior temporal and prefrontal cortices) were closely associated. The same analysis found that the amygdala separated into two parts (the basolateral complex; BL and the centromediaal complex; CM) which may have also functionally separated during the evolution of insectivores and prosimians. The hypothesis that the amygdala and the constituent parts of the amygdala (BL and CM complexes) are involved in coding social behaviour in the primate order was tested using brain volumetric and socio-ecological data (e.g. mean group size, % time grooming and diet composition), and compared using correlation and regression analyses. It is proposed that the basolateral amygdala functions

in anthropoid social behaviour, but probably not in prosimians. Finally, it is proposed that the connectional separation displayed for the two amygdala complexes (as revealed by NMDS analysis) will also be present when comparing amygdala component size with social variables, such as mean group size.

5.1 Introduction

The causes and consequences of the evolution of the primate (and therefore human) brain are one of the mysteries of modern science. Recent hypotheses have created debate in all disciplines concerned with evolutionary biology; anthropology, psychology, primatology, neuroscience and behavioural ecology. Work in this area is naturally made difficult by the fact that no one knows or will ever know exactly what did cause our (and our nearest relatives) brains to increase in complexity and size.

Evolutionary theory suggests that one or more "states" (ecological, social, technical, etc.) caused the brain to adapt for its increased complexity in primates and proto-hominids, or that the Environment of Evolutionary Adaptation (EEA) created selection pressures on primates which *required* them to evolve a more complex brain (Tooby and Cosmides 1992). Primates *could not* have evolved without a more complex brain. Many theories have been proposed as to what these "states" or EEA's were and at what point in time they were active.

One field which has failed to contribute considerably to this debate has been neurobiology. This is certainly not due to a scarcity of data, as Stephan's group has measured the brain (and brain part) volumes of large numbers of chiroptera, insectivores, prosimians and anthropoids (Stephan and Pirlot 1970, Stephan, Frahm and Baron 1981). Unfortunately, the only volumetric data has been provided by this one research group, and only on one representative from a species and in some cases from only one species in a genus. This does not take individual differences and variation into consideration. This is something that has been discussed by Stephan's group (Stephan et al 1981), but not by other primatologists using the data. No further data has been collected for obvious

reasons. Measuring the volumes of individuals is painstaking research, requiring patience for little rewards. Fortunately, new anatomical data from a few monkey and ape species is being collected using neuroimaging techniques such as MRI (Semendeferi et al 1997). These studies should provide results ultimately preferable to previous studies as they can be used to measure brains in living animals, thereby providing volumetric data untainted by histological methods which may substantially shrink brain tissue.

Theories of brain evolution have not taken into consideration neurobiological data concerning localisation of brain function. It is the purpose of this chapter to discuss relationships between the relative size of the amygdala and its component parts with socio-ecological measures. The cortico-basolateral division and lateral basal nucleus have a large number of anterior temporal and orbitofrontal cortical connections. The anterior temporal and orbitofrontal cortices contain cells which may function in social cognition and recognition, and lesions of cortex cause deficits in social, affiliative, emotional and aggressive behaviour (see Chapter II). The centromedial division by comparison has few cortical, but many subcortical connections, particularly with effector structures (hypothalamus, thalamus, brainstem and basal ganglia (Amaral et al 1992). The cortico-basolateral division therefore, is connected with areas involved in complex social behaviour, whereas the centromedial division is not.

Evolution of brain & intelligence: alternative hypotheses

Two schools of thought concern the driving forces behind the evolution of the primate brain. Both relate to adaptations to changes in the environment and the consequent effects on social behaviour, food abundance, etc. Ultimately, absolute brain size is constrained by the volume of space in the skull or cranial capacity and various anatomical features (such as vertebral column, muscles, ligaments, etc.) for keeping a large brain supported. A related factor is cranial blood flow. Bipedal posture necessarily moves the head higher relative to the ground, than a quadrupedal posture. Increased blood flow is required to produce the necessary supply of blood to this greater height and is also a requisite for an enlarged brain. Robust australopithecines and other extinct

hominids are said to have moved from the forests to the savannah (an environment with little protection from the sun). This environmental change and whatever behavioural consequences caused the brain to increase in size, would necessitate what Falk has called a "radiator" (Falk 1990) or an appropriate venous system which can allow increased blood flow and cool the brain. The venous system probably used by australopithecines and other hominids (hypothesised from venous patterns on brain endocasts and physiological studies of modern humans) is different from those used by apes (Falk 1992). There appears to be an evolutionary grade shift in the use of different venous systems from the jugular vein to the vertebral plexus (mastoid and parietal emissary veins). This shift in emphasis is commensurate with Falk's "radiator" argument.

This explanation may helps us understand the physiological and anatomical constraints imposed by brain enlargement. Evolution, however, does not predict what faculties will be of use in the future. A larger brain must have been an adaptation to an environmental or behavioural *requirement*. Change in posture required a better adapted venous system and this may have had the knock-on effect of permitting an enlarged brain.

There are other examples of physiological mechanisms which would allow for an increase in brain size. Martin (1996) suggests that brain development in the womb may be important in brain evolution. The 'maternal energy hypothesis' suggests that there is a strong relationship between the basal metabolic rate (BMR) of the mother and the size of her offspring's brain. The greater the energy transferred from mother to infant, the greater the brain size. The mother would therefore either be required to have a greater BMR (fuelled by highly digestible foods, such as fruit and meat), or increase the length of gestation. The mother would also require an enlarged pelvis for birth of a large brained infant.

A further argument for the effects of BMR has been proposed in the "expensive tissue hypothesis" (Aiello and Wheeler 1995). They suggest that as the enlarged brain is a metabolically expensive organ (20% of all energy resources in humans) other energy expensive organs such as the gastro-intestinal (GI) tract should reduce in size, thereby providing extra energy for the brain. This idea comes from data suggesting that there is no significant correlation between BMR and brain size in humans (Aiello and Wheeler

1995). The brain increases in size and requires extra energy but gross levels of energy required by the body are not necessary. It appears that the energy is found elsewhere in the body. Aiello and Wheeler state that a reduction in mass of one of the other energy expensive tissues would be sufficient to provide this extra energy. The evidence for the GI tract as the mass reducing organ is enticing. As brain mass increases there is a matched decrease in the mass of the GI tract and the resultant energy provided by this mass reduction is the same as that required by the increased brain mass. Other energy expensive organs have been ruled out of the equation. The liver replaces glucose levels which are required by an enlarged brain; the heart could not reduce the efficiency with which it pumps blood around the body (especially to a larger heart, see previous arguments) and the kidneys could not reduce in size as they are required in a savannah environment where water is scarce (also see earlier). Finally, a smaller gut requires a better diet of highly digestible foods (meat and fruit) and in smaller quantities to function in the same way as a larger gut.

Both the maternal energy and expensive tissue hypotheses suggest that better sources of food contribute to the brain's efficient functioning. This presupposes an environmental pressure to increase brain size throughout primate evolution. Such ecological pressures may have led to a primate specialisation for remembering, locating and extracting certain types of food (Byrne 1995a, b, 1997). Predominantly leaf-eating primates (such as howler monkeys or gorillas) are relatively unspecialized feeders. The preferred foods are widely available and do not appear to require any special cognitive skills to locate them (however see Byrne 1995a, Byrne and Russon 1997, who suggest that large primates can eat copious amounts of difficult to process foods). Gorillas in comparison to howler monkeys are substantially larger and require plentiful amounts of foliage to fuel their massive bulk.

Frugivorous or omnivorous primates (such as baboons, rhesus macaques and chimpanzees) are specialised feeders. Their diets rely on gaining higher quality food, such as fruit and meat which are patchily distributed. Unfortunately, high quality foods are spread over wide areas in clumped patches, and are not available all year (fruits are usually available for 2-3 month stretches, Milton 1988). Milton (1988) studied the

feeding ecology of two species of neotropical monkeys; spider and howler monkeys. Spider monkeys are different from howler monkeys as their diet is predominantly fruit based (60-72%). The spider monkey's home range size is 25 times that of howler monkeys (suggesting dispersed resources). The monkeys also differ in social structure; howler monkeys live in relatively large social groups who learn about the location of favourite trees from other group members, whereas spider monkeys live in small foraging units of a mother and infant. Information about feeding in spider monkeys could be transferred from mother to infant. As spider monkeys are primarily fruit-eaters their chosen food cannot sustain members of a larger social group (Milton 1988). Spider monkeys have to rely on their own skills to remember the location of good fruiting trees, when the trees produce optimal levels of fruit and whether newly encountered fruits are sufficient sources of nutrition. Milton (1988) has suggested that, in these two species at least, diet is correlated with mental ability, which would have required increased processing power. This increased power would itself require more and better sources of energy (see earlier).

At a basic level, this is seen in these two species. The spider monkey brain (107g) is twice the weight of the howler monkey brain (50.3g). Brain size is constrained by energy input; and this correlates well with diet. Gorillas, for example, have to eat large amounts of plant matter to gain the same nutritional value as eating a smaller amount of fruit. To do this, gorillas remain sedentary, thereby not expending energy, or utilise nutritious, but difficult to extract foods. (It is interesting to note that gorillas are not very sociable animals; sociality expends large amounts of energy).

Gibson (1986) and King (1986) both suggested that the extraction of difficult to procure foods has had an effect on primate brain and intelligence (although this is hard to reconcile with the data for gorillas who have relatively small brain and neocortex (Stephan et al 1981), but complex methods for extracting foods, Byrne and Byrne 1993, see also Russon 1997 for orangutan complex feeding skills). Difficult to extract, catch or well hidden foods such as fruits with tough skins, nuts, shellfish, eggs, snails insects and small animals are part of the diets of a large number of primates (other mammals, birds and reptiles). Procurement of these foods require special skills and heightened perceptual

and motor abilities (visual, auditory, olfactory and fine motor manipulation). What may differentiate some simian primates from other animals who eat these foods is fine motor control including use of tools. Thrushes may use stones to crack open snail shells, but the ability is not precisely controlled. Gibson (1986) tested the hypothesis that omnivorous extractive foragers had larger relative brain sizes (RBS, relative to body size) than other types of foragers. The smaller brained primates did not use extractive foraging and usually ate whole foods, such as fruit, leaves, grass or insects. It seems reasonable to suggest that extractive foragers are better adapted to changing environments than non-extractive foragers, by utilising unusual foods in times of scarcity.

Acquisition of various types of food suggest a need for enhanced sensory abilities. Barton et al (1995) studied correlations between certain sensory brain regions (visual brain; striate visual cortex, lateral geniculate nucleus, optic tract, and olfactory brain; olfactory bulb, piriform cortex and accessory olfactory bulb) in primates. They found that there appeared to be a trade-off between olfaction and vision, nocturnal species (not surprisingly) had larger olfactory bulbs and smaller striate cortices than diurnal primates. The reverse was true for the diurnal primates. Vision and olfaction are important for frugivores, who need to evaluate the location, toxicity, colour and smell of fruit). Surprisingly, there was no correlation between percentage fruit in the diet of diurnal haplorhines and the volume of visual and olfactory structures. There was a correlation between percentage fruit in diet and volume of olfactory structures but not visual structures in nocturnal strepsirhines. Vision and olfaction appear unimportant for folivores.

It remains to be seen which ecological and behavioural pressures caused an expansion in brain complexity. The complexity of social life has been proposed as one answer. Chapter II discussed some of the reasons why living in large groups would be beneficial. Territoriality, intrasexual competition, predator pressure, food density and food distribution are some of the suggested factors effecting group size (van Schaik and van Hoof 1983). Ecological variables are at the forefront of the list of pressures warranting larger groups (but not necessarily complexity of relationships within a group).

Several authors (Dunbar 1992, Sawaguchi 1992, Barton 1996, Barton and Dunbar 1997) have suggested that increasing the size of a group requires more computational power (reflected as an increase in the number of neurons and the connections between them) to keep track of the fluctuating state of relationships. Humphrey (1976) and Jolly (1966) were the first to discuss issues of intelligence in terms of social behaviour. The "social" or "Machiavellian" intelligence hypothesis stated that an increase in intelligence (and therefore brain processing capacity) was required to process the complex relationships inherent in living a social existence. For discussions of the merits of the social intelligence hypothesis, see Chapter II.

Comparative neuroanatomical and socio-ecological analyses appear to be ideal for testing this hypothesis; short of detailed experiments and observations on a large number of primate species. The behavioural ecology of a large number of primates is known and a large set of anatomical data is present for the majority of brain structures in each of these species. The rationale behind the tests described in the final part of this chapter are discussed. The next section reviews the analyses performed so-far and the limitations of these particular analyses for answering questions of how particular brain structures solve social problems. Following this, the final section of the chapter provides the development of the tests.

Armstrong et al (1987) were the first to find an evolutionary relationship between brain size and social system. They compared the mean values of anthropoid thalamic nuclei depending with male social system (monogamous, harem, dominance hierarchy or fission-fusion). Although, they had the insight to look at the size of brain components rather than whole brain size, the choice of brain area was related to functional or anatomical data (as no evidence as to the contribution of the thalamic nuclei to social behaviour has been reported). Armstrong et al found that multi-male groups had larger anterior thalamic nuclei (and more neurons in these structures) than single-male groups.

Sawaguchi (1990, 1992, Sawaguchi and Kudo 1990) also attempted to correlate measures of social behaviour and ecology with measures of brain anatomy using the comparative method. Sawaguchi and Kudo (1990) studied sociality at a basic level; whether a species was solitary, monogamous and polyandrous (multi-male) or

polygynous (multi-female). The data from the different species were grouped at the level of genus so that species with similar ecological and social parameters were grouped together. The neuroanatomical data used was neocortex volume, or brain weight (removing the effect of body weight). Sawaguchi found no difference between groups due to activity timing, but there was a positive significant correlation between neocortex size and troop size (in prosimians). In anthropoids, polygynous groups had larger neocortices than monogynous groups. The effect of diet and social structure on relative brain size (RBS) was studied more extensively by Sawaguchi (1990). Four categories of diet (frugivorous, frugivorous/omnivorous, folivorous or "seed-grass" eating) and five categories of social structure (solitary, monogynous, single-male polygynous, multi-male polygynous or variable male polygynous) were analysed with 42 generic groups. Frugivorous *Ceboidea* RBS correlated with troop size and folivorous *Cercopithcoidea* RBS correlated with home range size.

Sawaguchi (1992) used measurements of relative neocortex size (RSN), "the difference between actual neocortical volume and the volume expected for an allometric relationship between neocortex volume and volume of the rest of the brain" (pp. 131). The possibility of ancestral affinity was compensated for by analysing ecological and social measures at the subfamily and genus levels. Ecology was studied at a gross level by grouping folivores and frugivores separately, time of activity (nocturnal or diurnal) and stratification (arboreal or terrestrial) separately. Sociality was compared across monogynous and polygynous groups. There was no difference in RSN between polygynous and monogynous groups at the subfamily level, however differences did occur when the influence of ecological measures were removed. Frugivorous species had a higher RSN than folivorous species, polygynous/frugivorus genera had a higher RSN than monogynous/frugivorous genera and polygynous/frugivorous/arboreal subfamilies had a higher RSN than monogynous/frugivorous/arboreal subfamilies. There was no difference between arboreal and terrestrial primates on any other measures. When RSN was compared with home range size (as an indicator of mental complexity associated with diet) and troop size (as an indicator of mental complexity associated with social

behaviour) there was a significant correlation for all anthropoids and Ceboidea (for troop size only).

This last result has been replicated on a number of occasions (Dunbar 1992, Barton and Purvis 1994, Barton 1996). There appears to be no significant association between the size of the neocortex and ecological variables (such as diet or home range size). This data suggests that the neocortex did not evolve to process information about processing food (although this cannot be ruled out from a small amount of studies). It is probable that the processing power required to locate and extract food is small in comparison to the power required to furnish social relationships.

Dunbar (1992) attempted to determine what precisely was the driving force behind primate brain evolution. Dunbar used volumes of the primate neocortex, suggesting that "intelligence" requires increased processing and that a larger computer can store the largest amount of information. This is not completely true as the processing power of modern computers is not constrained by physical size. A laptop computer may have a larger processing power compared to a desktop computer, if the number of components have increased complexity or the number of components are increased; e.g. Pentium > 486 > 386. Connectional complexity is the key (as size may remain the same, but the network of connections increases, Holloway (1966). Dunbar (1992) used neocortex ratio (NR; against the volume of the rest of the brain) as an anatomical variable, because the neocortex may be the seat of cognition, and lesions of different parts of the neocortex effect social behaviour (see Chapter II for a review). Comparing NR with mean group size (after removing the effects of body size) produced a significant correlation ($r^2 = 0.764$, $p<0.001$), whereas comparing NR with ecological variables produced the following results, % fruit in the diet (no correlation), home range area ($r^2 = 0.593$) and day journey ($r^2 = 0.295$). The effects of body size and group size were removed and produced positive correlations between NR and % fruit in diet (Pairwise $r = 0.503$, $p < 0.05$) and range area (Pairwise $r = 0.793$, $p < 0.05$) but not day journey (Pairwise $r = 0.294$, $p > 0.05$). The differences of NR were also tested at the group level between extractive versus non-extractive foragers (see also Gibson 1986). Extractive foragers (as a group) had a significantly larger NR than non-extractive foragers.

The regression equation for predicting the NR (neocortex ratio) developed from this study was developed further by Aiello and Dunbar (1993), who used it to predict the group size (and percentage grooming time) of extinct hominids. Fossil endocasts of extinct hominids can be used to evaluate and determine cranial capacity. From these values, Aiello and Dunbar produced further regression equations to predict NR for extinct species. Using these measurements they suggested that increased group size and amount of grooming required to furnish social relationships required a communication system such as language. The arguments are a little circular as large groups require a better communication system (i.e. language). Language requires a more complex brain system to operate it and a more complex brain enables formation of larger groups, etc.

The NR regression equation (Aiello and Dunbar 1993) may have been overly interpreted, and has been used extensively by Dunbar and colleagues (Dunbar 1995, Dunbar and Joffe 1997, Pawlowski et al 1997 and Dunbar and Bever 1997). Uses have included predicting the neocortex ratio for species which were not included in the original Stephan et al (1981) anatomical data set. Strangely, the equation has been used sometimes to the exclusion of real data. From this new data, Dunbar (1995) has suggested that there are differences in NR between four categories of foragers (skilled, unskilled, specialised and non-extractive), that prosimian NR is related to mean group size (Dunbar and Joffe 1997, $r^2 = 0.278$, $p < 0.05$), that the mating and social skills of group males (Pawlowski et al 1997) is related to NR (groups with 2-4 males, $b = -0.075$, $p = 0.697$; groups with 5-8 males, $b = -1.289$, $p < 0.01$; groups with 9-20 males, $b = -0.629$, $p < 0.05$) and that NR of insectivores and carnivores (Dunbar and Bever 1997) is significantly correlated with mean group size (insectivores, $r^2 = 0.295$, $p < 0.05$ and carnivores, $r^2 = 0.288$, $p < 0.05$). The problem with using this neocortex equation is that it is based on a correlation of a regression.

A new comparative method for analysing data from closely related species has been used to determine an association between sociality and brain size. The method is discussed fully in the methods section. Briefly, the method treats individual data points from separate species as possibly being evolutionarily related. It is highly probable that a certain trait (morphological or behavioural) is mutual to two related species with a

common ancestor. The comparative method uses phylogenetic data on the similarity (and dissimilarity) of species (using branch lengths of time since splitting from the common ancestor). This information is then used to compute contrasts of anatomical and/or behavioural data, which can then be analysed using normal statistical methods. Barton and Purvis (1994) used this method to test relationships between brain volume data and socio-ecological data (group size and home range size). They found that absolute volumes of the cerebellum, medulla, mesencephalon, diencephalon, telencephalon and whole brain correlated well ($r > 0.67$) with body weight, group size and home range size. They therefore suggested that there were no selection pressures on large *specific* brain systems. They then looked at smaller systems; neocortex and hippocampus. Neocortex as a system for processing large amounts of information and hippocampus for memory functions. They found that correlating contrasts of the relative size of these two structures (against the rest of the brain) produced significant correlations between neocortex and group size ($r = 0.96$, $p < 0.001$), but not home range size, and between hippocampus and home range size ($r = 0.97$, $p < 0.05$), but not group size. This suggests that the neocortex is used in remembering social relationships and the hippocampus is used in remembering the location of food.

Finally, Barton (1996) used the comparative method to determine whether there was a difference in the correlation with neocortex ration between diurnal and nocturnal primate groups. Barton found that contrasts in neocortex ratio correlated with contrasts in group size for diurnal primates and that the correlations were significant only for haplorhines, not for strepsirhines (this is not surprising as the majority of strepsirhines are nocturnal).

Measures of social complexity

Social complexity is an almost impossible variable to measure particularly when comparing between a large number of primate species. Whiten and Byrne (1988b) suggest that every animal in a troop has to know not only its own relationships, but the relationships between dyads, and even triads (third party relationships). They suggest that

this would be a power function of group size. Byrne (1995b) suggested an equation for the possible number of dyadic relationships in a group, ΣN from 0 to (N-1) where N is the group size.

Maximum group size may be a good indicator as to the upper limits of social complexity. The maximum number of individuals in a group present the highest levels of relationship processing. It is extremely unlikely, however, that any primates know all members of their troop and certainly not the precise details of all triadic (or even dyadic) relationships. Most primates remain in small group units (or cliques) within a troop (Dunbar 1996b) and these units may be better indicators of social complexity (Kudo et al 1997). It is also difficult to determine clique sizes for all species of primates, and such data is not available in the published literature except for a few representative species.

Aims and predictions

The method used in Chapter IV analysed simple brain connection data to determine whether the regions of the macaque brain that were said to function in coding social behaviour were anatomically associated and whether connections between areas determined functionality. The amygdala, anterior temporal cortex, prefrontal cortex, cingulate cortex and schizocortex all grouped together suggesting similarity between their connection patterns. This also suggested similarity in function. One striking result was the parcellation of the amygdala into two distinct nuclear groups, the basolateral (BL) and the centromedial (CM). This separation had been proposed earlier by Johnson (1923) on anatomical and cytoarchitectural bases. The subsequent analysis provides evidence for the following hypotheses based on the connectional analysis in Chapter IV and the neurobiological data described in detail in the literature review of Chapter II. First, the two divisions of the amygdala will correlate with social group complexity. Second, the correlations will differ between the two complexes, which may reveal differences in function. Three, no component of the amygdala will correlate with any ecological variable.

5.2 Methods

5.2.1 Anatomical data

Volumetric brain measurements were taken from published sources; Stephan et al (1981) for volume of the whole brain and Stephan et al (1987) for volume of the amygdala and component parts of the amygdala. The components of the amygdala analysed were cortico-basolateral complex (lateral basal, medial basal, accessory basal, lateral and cortical nuclei, for abbreviations see Chapter III, IV), centromedial complex (central and medial nuclei and periamygdaloid complex) and the lateral basal nucleus (magnocellular basal nucleus of the amygdala, Stephan et al 1987). The cortico-basolateral complex (BL) is slightly different from the basolateral complex described in the previous chapter, because of the addition of the cortical nucleus, which traditionally is associated with the centromedial complex (CM). The volume of the cortical nucleus was not presented in the original Stephan et al data set, so the cortical nucleus is included with the rest of the BL complex through necessity.

Data is presented for 18 representative species of prosimians (strepsirhines), and 26 species of simian primates (haplorhines; New and Old World monkeys, lesser and greater apes). These species were chosen because of the original volumetric data of Stephan et al (1981, 1987). Data from *Homo sapiens* was not included, as no reliable socio-ecological data was present for humans. *Pygathrix nemaeus* (Douc langur) was removed from the socio-cognitive analyses as no data could be found about this species' social system or behaviour in the primatological literature.

The effect of body size (mass) was removed from subsequent analyses using two methods. First, the effect of mass was regressed against the volume of the amygdala/brain component. The residuals from the regression line were then used in the analysis with socio-ecological variables. A second method indirectly removed the effects of body weight, by regressing the rest of the amygdala/brain against a corresponding component part. For example, the amygdala has two divisions; the BL and CM complexes. When testing the relationship between the BL complex and a socio-ecological variable, the possible effects of the CM complex (due to the inter-connectivity between the two

divisions) were removed by regressing the volume of the CM complex against the volume of the BL complex. Again, the residuals from the regression line were then used in an analysis of the relationship between BL and socio-ecological variables. For other analyses, the CM complex was regressed against the BL complex, the LB nucleus against the rest of the amygdala (amygdala minus LB nucleus, RoA), the amygdala against the rest of the brain (brain minus amygdala, RoB) and the rest of the brain against the amygdala.

5.2.2 Socio-cognitive data

Socio-cognitive variables were taken from published sources. Four measures of social complexity were analysed. First, mean group size is a conservative measure of the number of possible relationships with which an individual may have to keep track of. Second, the mean number of females in a group is a good indicator (certainly for anthropoids) of the breeding capabilities of a group. (Female oriented groups are the hallmark of "fission-fusion" societies such as chimpanzees, where the males stay in the group until young adulthood and then leave to try their reproductive skills elsewhere.) Mean group size measures were taken from Smuts et al (1987) and Dunbar (1992). The number of females in a group were taken from Dunbar (1992).

A third more general measure of social behaviour used was social system depending on the number of males (single or multi-male) in a group. These measures were whether the single-male groups were monogamous or harem and the multi-male groups were dominance-stratified or fission-fusion. These relationships were taken from Armstrong et al (1987).

The final measurement of group cohesion may be percentage time spent grooming (either grooming another or being groomed). Grooming has been suggested to not only be used for cleansing purposes, but is also a main channel for diffusing aggressive encounters, reconciliation (de Waal 1989) and creating and maintaining friendships (Dunbar 1991).

5.2.3 Ecological data

A series of data concerning ecological factors were also derived from published sources. Five measures were used to test the ecological hypothesis of primate intelligence, the percentage of fruit in the diet, mean home range size, stratification or ecological niche (arboreal, A; semi-terrestrial, ST; or terrestrial, T); diet type (folivorous, Fol; frugivorous, Frg; or insectivorous, Ins) and activity timing (nocturnal, Noc or diurnal, Dl). These data were taken from Clutton-Brock and Harvey (1977), Smuts et al (1987), Dunbar (1992) and Barton et al (1995).

5.2.4 Data analysis

The brain and socio-ecological data sets were analysed using three methods. First, relationships between brain volume (removing the effects of body size) and socio-ecological variables were analysed using linear regression (and ANOVA).

Second, the data was analysed by socio-ecological variable using ANOVA and *post-hoc* tests (Protected Least Significant Difference, PLSD). The variables compared were social grouping, (small, medium or large groups), male group composition and diet type (by averaging data for all species in each group). Finally, categorical data (activity type, average of all species in each group {nocturnal or diurnal}and stratification, average of all species in each group {arboreal or terrestrial}) was analysed using student t-tests (unequal variance).

All raw data is displayed in Table 5.1 (a-c). Table 5.1 (a) displays the raw volumetric data for LB, BL, CM, RoA, amygdala, RoB and whole brain (in mm3). The socio-cognitive data is displayed in Table 5.1 (b); mean group size, number of females, male social structure and percentage grooming time. The body mass and ecological data is displayed in Table 5.1 (c); activity timing, diet type, percentage fruit in diet, stratification and home range size.

The possible effects of ecological variables on socio-cognitive data and the effects of socio-cognitive variables on ecological data, were eliminated by regressing the effects of percentage fruit and home range size respectively against the three socio-cognitive

Table 5.1 (a): Volumetric data of amygdala, basolateral complex (BL), centromedial complex (CM), lateral basal nucleus (LB), whole brain, rest of amygdala (amygdala minus LB nucleus) and rest of brain (brain minus amygdala), in mm2 for Strepserhine and Haloprhine primates.

Genus	species	Amyg	BL	LB	CM	Brain	RoB	RoA
Microcebus	*murinus*	36.6	24.5	2.1	12	1680	1643.4	34.5
Cheirogaleus	*major*	102.3	68.8	8.8	33.6	4667	4564.7	93.5
Cheirogaleus	*medius*	64.9	40.8	3.9	24.1	4667	4602.1	61
Petterus	*fulvus*	260.7	185.5	20	75.2	25910	25649.3	240.7
Varecia	*variegata*	368.2	253.5	22.9	114.7	25910	25541.8	345.3
Lepilemur	*ruficaudatus*	133.9	91.4	7.8	42.5	7175	7041.1	126.1
Avahi	*laniger*	113.2	73.8	5.4	39.5	9461	9347.8	105.4
Propithecus	*verreauxi*	302.2	206.4	22.5	95.8	25194	24891.8	279.7
Indri	*indri*	398.5	277.7	26	120.8	36285	35886.5	372.5
Daubentonia	*madasgascariensis*	481.7	357.1	25.3	124.6	42611	42129.3	456.4
Loris	*tardigradus*	104.1	72.5	6	31.6	6269	6164.9	98.1
Nycticebus	*coucang*	189.2	121.4	11.4	67.8	11755	11565.8	177.8
Perodictus	*potto*	202.2	138.8	14.1	63.5	13212	13009.8	188.1
Galago	*senegalensis*	73.2	51.5	4.2	21.7	5794	5720.8	69
Otolemur	*crassicaudatus*	148.8	103.3	8.5	45.5			140.3
Galagoides	*deidoff*	57.9	40.4	3.2	17.6	5794	5736.1	54.7
Tarsius	*bancanus*	53.4	39.7	3.3	13.7	3393	3339.6	50.1
Callithrix	*jacchus*	106.1	75.6	7.7	30.5	7241	7134.9	98.4
Cebuella	*pygmae*	75.4	57.9	7.1	17.5	4302	4226.6	68.3
Saguinus	*midas*	144.9	106.1	8.8	38.8	9537	9392.1	136.1
Saguinus	*oedipus*	141.8	110.2	11.4	31.6	9537	9395.2	130.4
Callimico	*goeldii*	146.9	111.2	11.6	35.6	10510	10363.1	135.3
Cebus	*albifrons*	458.2	337.8	36	120.4	66939	66480.8	422.2
Aotus	*trivirgatus*	193.6	136.9	14.6	56.6	16195	16001.4	179
Callicebus	*moloch*	254.1	179.5	16.3	74.6	17944	17689.9	237.8
Saimiri	*sciureus*	242.4	188.3	15.5	54.1	22572	22329.6	226.9
Pithecia	*monacha*	365.3	273.7	31.7	91.6	32867	32501.7	333.6
Alouatta	*seniculus*	426	324.3	31.4	101.7	49009	48583	394.6
Ateles	*geoffroyi*	868.8	644.5	74.7	224.3	101034	100165.2	794.1
Lagothrix	*lagothricha*	753.2	565.2	74.6	188	95503	94749.8	678.6
Macaca	*mulatta*	678.4	493.2	69.7	185.2	87896	87217.6	608.7
Cercocebus	*albigena*	781.3	515.9	83.5	265.4	97603	96821.7	697.8

Papio	*anubis*	953.5	740.2	104.7	213.3	190957	190003.5	848.8
Cercopithecus	*ascanius*	572.5	433.2	45.6	139.3	67035	66462.5	526.9
Cercopithecus	*mitis*	704	493.1	66.4	210.9	67035	66331	637.6
Miopithecus	*talapoin*	413.1	311.3	52.9	101.9	37776	37362.9	360.2
Erythrocebus	*patas*	688.4	489	63.7	199.4	103167	102478.6	624.7
Colobus	*badius*	500.9	377.3	47.7	123.6	73818	73317.1	453.2
Pygathrix	*nemaeus*	489.2	337.5	51.2	151.6	72530	72040.8	438
Nasalis	*larvatus*	718.9	499.1	55.8	219.8	92797	92078.1	663.1
Hylobates	*lar*	666.2	510.2	84.6	156	97505	96838.8	581.6
Pan	*troglodytes*	1421.8	1046.5	136	375.3	382103	380681.2	1285.8
Gorilla	*gorilla*	2752.6	1998.1	227.5	754.5	470359	467606.4	2525.1

Table 5.1 (b): Raw socio-cognitive data for Strepserhine and Hapolorhine primates (Data taken from Clutton-Brock and Harvey (1977, 1980), Smuts et al (1987) and Dunbar (1992). Male group structure, SM-M, single-male monogamous; SM-H, single-male harem; MM-DS, multi-male dominance stratified; MM-FF, multi-male fission-fusion. Male group structure was taken from Armstrong et al (1987).

Species	Mean Group Size	Number of Females	Grooming (% time)	Male Group Structure
Microcebus murinus	1	1		
Cheirogaleus major	1	1		
Cheirogaleus medius	1	1		
Petterus fulvus	9.5		5	
Varecia variegata	2	1		
Lepilemur ruficaudatus	1	1		
Avahi laniger	2	1	2	
Propithecus verreauxi	5	1	4.7	
Indri indri	4.3	1	1	
Daubentonia madagascariensis	1	1		
Loris tardigradus	1	1		
Nycticebus coucang	1	1		
Perodictus potto	1	1		
Galago senegalensis	1	1		
Otolemur crassicaudatus				
Galagoides demidoff	1	1		
Tarsius bancanus	1	1		
Callithrix jacchus	8.5	2.5		SM-M
Cebuella pygmae	6	1		
Saguinus midas tamarin	5.2	2.4		SM-M
Saguinus oedipus	5.2	2.4		
Callimico goeldii	7.3	1		
Cebus albifrons	18.1	5.7	0	
Aotus trivirgatus	3.8	1		SM-M
Callicebus moloch	3.3	1	0.1	
Saimiri sciureus	32.5	7.9	1.5	MM-DS
Pithecia monacha	3.6	1		
Alouatta seniculus	8.2	3.6	0.4	MM-DS
Ateles geoffroyi	17	9.8	7	MM-FF
Lagothrix lagothricha	23.4	7.5		MM-FF
Macaca mulatta	39.6	14.3	15	MM-DS
Cercocebus albigena	15.4	7	5.8	MM-DS
Papio anubis	52.1	11.4	12.2	MM-DS

Cercopithecus ascanius	23.9	8.2		SM-H
Cercopithecus mitis	23.9	8.2		
Miopithecus talapoin	65.5	15.4		MM-DS
Erythrocebus patas	28.1	7.9		
Colobus badius	50	33.3	3.8	SM-H
Pygathrix nemaeus				
Nasalis larvatus	14.4	6.3		
Hylobates lar	3.4	1	2.1	SM-M
Pan troglodytes	53.5	13	6.2	MM-FF
Gorilla gorilla	7	3	1	MM-DS

Table 5.1 (c): Raw ecological data for Strepserhine and Haplorhine primates. Diet types, FR = frugivorous, FO = folivorous, IN = insectivorous. Stratification, A =arboreal, T =terrestrial. Activity, N = nocturnal, D =diurnal, Home Range = km2, Body Mass = g

Species	Diet	% Fruit	Stratification	Activity	Home Range	Body Mass
Microcebus murinus	FR		A		1.035	0.005
Cheirogaleus major	FR		A	N	4	0.031
Cheirogaleus medius	FR		A	N	4	0.031
Petterus fulvus	FR		A	D	11.875	2.2
Varecia variegata	FR		A	D		2.2
Lepilemur ruficaudatus	FR	5	A	N	0.2	0.92
Avahi laniger	FR	0	A	N		1.07
Propithecus verreauxi	FO	40	A	D	5.25	3.48
Indri indri	FO		A	D	17.85	6.25
Daubentonia madagasariensis	IN		A	N		2.8
Loris tardigradus	IN	15	A	N		0.322
Nycticebus coucang	IN	60	A	N		0.8
Perodictus potto	FR	75	A	N	23	1.15
Galago senegalensis	FR		A	N	13.65	0.372
Otolemur crassicaudatus	FR	16	A	N		
Galagoides demidoff	IN	19	A	N	1.6	0.372
Tarsius bancanus	IN	0	A		1.5	0.125
Callithrix jacchus	FR	14	A	D	0.3	0.28
Cebuella pygmae	FR		A	D		0.14
Saguinus midas tamarin	FR		A	D	25.4	0.38
Saguinus oedipus	FR		A	D		0.38
Callimico goeldii	FR		A	D	132.5	0.48
Cebus albifrons	FR	17	A	D	10	3.1
Aotus trivirgatus	FR	46	A	D	4.25	0.83
Callicebus moloch	FR	53	A	D	141.5	0.9
Saimiri sciureus	FR		A	D	7	0.66
Pithecia monacha	FR	82	A	D	14.5	1.5
Alouatta seniculus	FO	31	A	D	107.5	6.4
Ateles geoffroyi	FR	77	A	D	400	8
Lagothrix lagothricha	FR	79	A	D		5.2
Macaca mulatta	FR	63	T	D	160.5	7.8
Cercocebus albigena	FR	64	A	D	1357.5	7.9
Papio anubis	FR	32	T	D	29	25
Cercopithecus ascanius	FR	50	A	D		4.85
Cercopithecus mitis	FR	54	A	D		4.85
Miopithecus talapoin	FR	54	A	D	4200	1.2
Erythrocebus patas	FR	76	T	D	100	7.8
Colobus badius	FO	22	A	D		7
Pygathrix nemaeus	FO		A	D		7.5
Nasalis larvatus	FO	39	A	D	49	14
Hylobates lar	FR	60	A	D	200	5.7
Pan troglodytes	FR	66	T	D	20	46
Gorilla gorilla	FO	3	T	D		105

variables. The residuals were then regressed against the residuals of brain area (controlling for effects of body mass).

5.2.5 Independent contrasts (CAIC)

Recently, some authors have suggested that comparing data sets as independent variables is incorrect for analyses of evolutionary data (Harvey and Pagel 1991, Purvis and Rumbaut 1995, Barton 1996). The argument follows that a trait in one species may be shared by closely related species. For example, a lemur and a human are distantly related, but have a similar number of traits (four limbs, hands, two forward facing eyes, etc.). Chimpanzees and humans are more closely related (with a common ancestor at 6-8 million years ago). Chimpanzees and humans also share a large number of these same traits, but the probability that they were derived from the same common ancestor is greater than the traits shared between lemurs and humans. Comparison of independent contrasts removes the possibility of relatedness between species (and therefore traits) being overlooked in gross analyses of multiple related species. This method uses phylogenetic reconstructions of genera in analysis (and branch lengths or lengths of time since a common ancestor). The cladistic (and phylogenetic) reconstruction for the primate order has recently been developed by Purvis (1995).

A particular method used to compare independent contrasts (Harvey and Pagel 1991, as based on Felsenstein 1985), is a computer package called *Comparative Analysis of Independent Contrasts* (CAIC, Purvis and Rumbaut 1995). This package computes contrasts of any set of data for a species depending on the relationship with other closely related species. This method is used mainly in analyses of closely related species (such as within the primate order), but it may not be particularly useful when comparing across orders or sub-families. The output contrasts are analysed using normal statistical methods such as correlation and regression.

The main results of this chapter will not be analysed using the CAIC program. For the majority of primate genera in the sample, data from only one species is represented. Only three geni (*Cheirogaleus, Saguinus* and *Cercopithecus*) have more

than one species (i.e. 2) represented. For example, of the large number of macaque species, only *Macaca mulatta* is represented. The independence of species is, therefore likely to be high, especially between distantly related species, for example, *Gorilla gorilla* and *Indri indri*. The relationship between the BL complex and group size, and between the CM complex and group size have been analysed using CAIC. No differences were found when compared with results from analyses not using CAIC (see Results section for CAIC results). [1]

5.3 Results

Correlations were performed between the raw anatomical data (amygdala, BL, CM, LB, BL (-LB), RoA and whole brain, to determine the relationships between brain regions. The correlation coefficients are displayed below in Table 5.2. All areas were highly significantly correlated. These results suggest that any significant correlations between area X and a socio-ecological variable may be due to the relationship between the two variables, not because of a general increase in brain size (Findlay and Darlington 1995) or the level of connectivity between two areas (including area X). For example, the volume of area X is highly correlated with the volume of area Y ($r^2 = 0.81$). The relationship between area X and number of copulations/hour reveals a significant correlation. There is no correlation between area Y and number of copulations/hour. The relationship between area X and copulations/hour is independent of the effects of area Y. This is justified by regressing area Y on area X and correlating the resulting residuals against copulations/hour.

---

[1] I wish to thank Robert Barton for analysis using CAIC. The CAIC method was recently brought to my attention after the main results of this chapter were written up. Attempts to use CAIC have failed, due to software problems.

Table 5.2. Correlation statistics (coefficients, r^2) for relationships between brain area volumes, amygdala, whole brain (brain), brain - amygdala (rest of brain, RoB), amygdala - LB nucleus (rest of amygdala, RoA), LB nucleus, BL complex and CM complex. All R square values were significant, $p < 0.00001$.

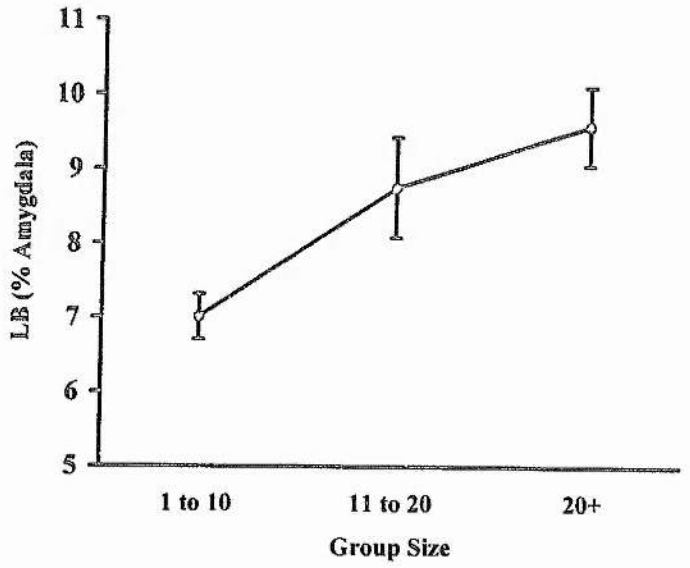
	Brain	RoB	Amygdala	RoA	BL	CM	LB
Brain	*1.00*	*0.75*	*0.71*	*0.70*	*0.72*	*0.67*	*0.75*
RoB		*1.00*	*0.91*	*0.91*	*0.92*	*0.88*	*0.90*
Amygdala			*1.00*	*1.00*	*1.00*	*0.99*	*0.96*
RoA				*1.00*	*1.00*	*0.99*	*0.95*
BL					*1.00*	*0.97*	*0.96*
CM						*1.00*	*0.94*
LB							*1.00*

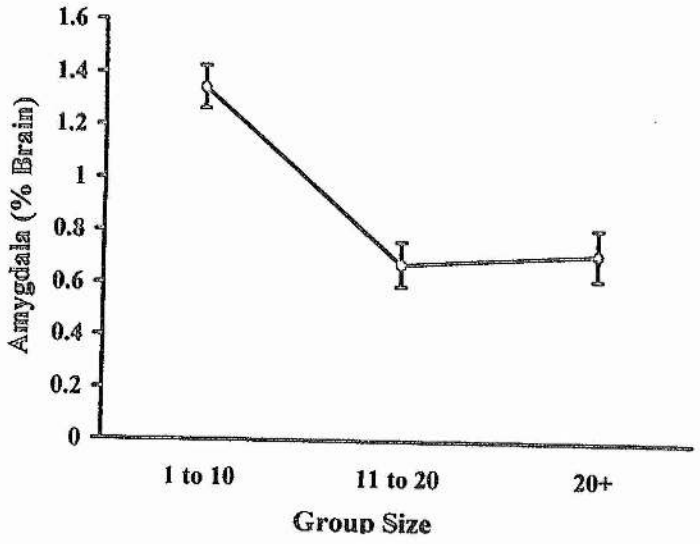
5.3.1 Social cognition

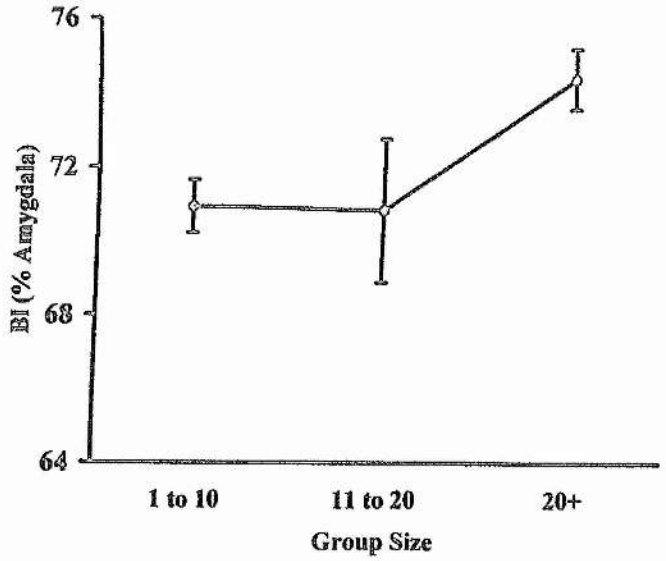
The LB nucleus was larger in groups with sizes greater than 11, $F(2,41) = 10$, $p < 0.001$; PLSD, $p < 0.05$. There was no difference between large and medium groups (PLSD, $p = 0.32$). There was an overall effect of the BL complex on group size, $F(2,40) = 3.63$, $p < 0.05$ and an almost significant effect between large and medium sized groups, PLSD, $p = 0.06$. There was an overall effect of the CM complex on group size, $F(2,40) = 3.52$, $p < 0.05$, but no significant differences between sizes of groups. There was a significant overall effect of group size on the size of the amygdala, $F(2, 38) = 13.1$, $p < 0.001$, with groups of 1-10 having relatively larger amygdalae than larger groups; medium group, PLSD, $p < 0.001$ and large group, PLSD, $p < 0.01$. All significant results are displayed as line graphs in Figure 5.1.

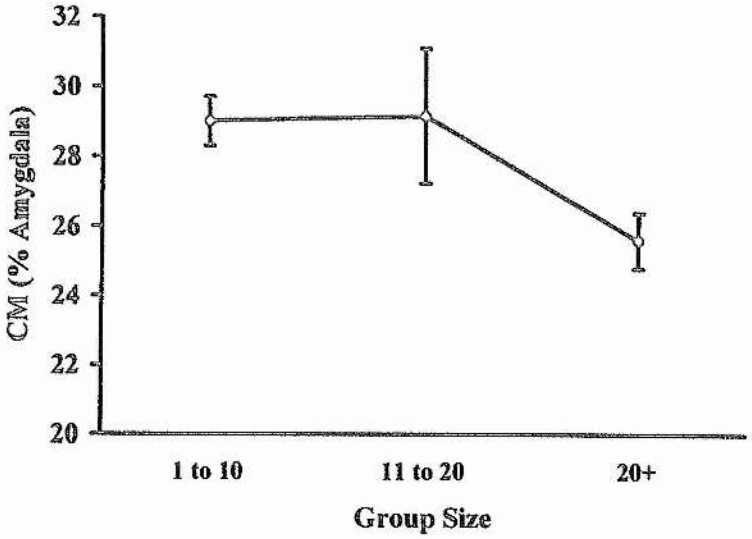
The second test for social complexity placed anthropoid (only) species data into categories dependent on male social structure (single-male versus multi-male groups). These two categories were further divided depending on the specific structure (see Table 5.3 for means and SEM's of each brain structure in each category). There was no overall effect of male group composition for the LB nucleus, $F(3,13) = 0.25$, $p = 0.86$, the BL

Figure 5.1. (a) Graph depicting differences between the mean percentage size (+/- SEM) of the lateral basal nucleus, LB (as a percentage of the amygdala) for 44 primate species (strepsirhines and haplorhines), where each species has been grouped dependent on group size. Using addition of percentages removes the effects of body mass. Small groups have been designated as groups containing 1-10 individuals, medium groups as containing 11-20 individuals and large groups as containing greater than 20 individuals. The size of the groups were arbitrary measures. (b) Graph depicting differences between the mean percentage size (+/- SEM) of the whole amygdala (as a percentage of the brain) using the same criteria as in (a). (c) Graph depicting differences between the mean percentage size (+/- SEM) of the basolateral complex, BL (as a percentage of the amygdala) using the same criteria as in (a). (d) Graph depicting differences between the mean percentage size (+/-SEM) of the centromedial complex, CM (as a percentage of the amygdala) using the same criteria as in (a).






76
72
68
64
BI (% Amygdala)
1 to 10
11 to 20
20+
Group Size


32
30
28
26
24
22
20
CM (% Amygdala)
1 to 10
11 to 20
20+
Group Size

complex, $F(3,12) = 0.3$, $p = 0.83$, the CM complex, $F(3,12) = 0.29$, $p = 0.83$ or the amygdala, $F(3,12) = 0.83$, $p = 0.5$.

Table 5.3. Means and SEM's for LB nucleus, BL complex, CM complex and amygdala grouped according to male social structure in anthropoid primates (Armstrong et al 1987).

	SINGLE-MALE		MULTI-MALE	
	Monogamous	*Harem*	*Dominance-stratified*	*Fission-Fusion*
Lateral Basal Nucleus				
Mean	**8.4**	**8.75**	**9.51**	**9.37**
SEM	1.47	0.75	0.85	0.39
Basolateral Complex				
Mean	**72.95**	**75.5**	**74.01**	**74.27**
SEM	1.33	0.2	1.55	0.41
Centromedial Complex				
Mean	**27.03**	**24.5**	**26**	**25.73**
SEM	1.31	0.2	1.55	0.41
Amygdala				
Mean	**1.07**	**0.77**	**0.67**	**0.67**
SEM	0.34	0.09	0.12	0.15

The relationships between brain components and social behaviour were tested further by correlating with more stringent socio-cognitive variables. The results (correlation coefficients, probabilities and ANOVA's) are presented in detail in a number of the tables below.

First, the results produced by regressing body mass against brain region are presented. Second, the results of regressing against the opposite brain region are presented (e.g. removing the effects of the CM complex from the BL complex). After removing the effects of body mass, all brain areas were significantly correlated

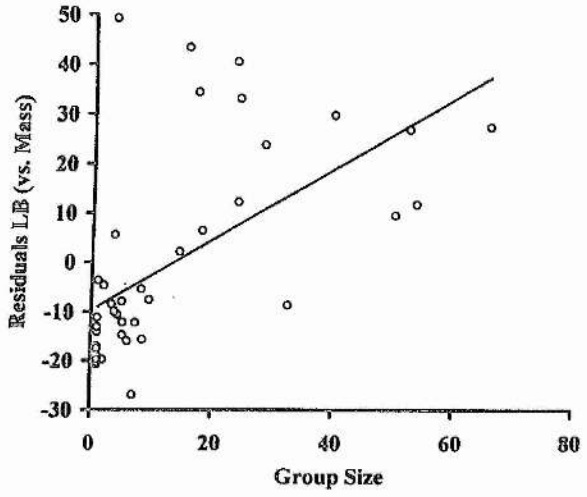
(positively) with mean group size (see Table 5.4 below). Scatter-plots demonstrating the relationships between group size and brain region are displayed in Figure 5.2).

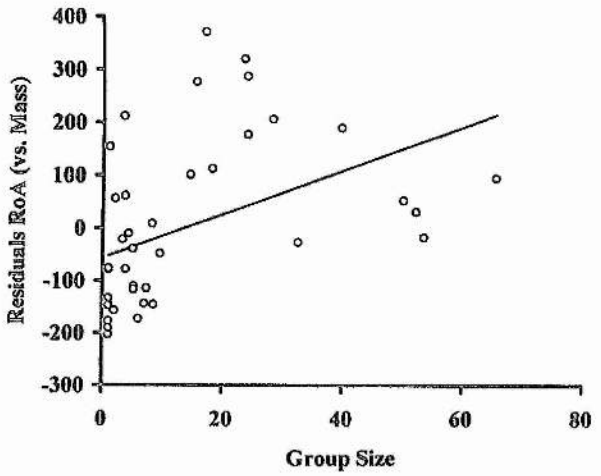
Table 5.4. Regression statistics for relationships between mean group size and volume of brain area (controlling for the effects of body mass on volume of brain area).

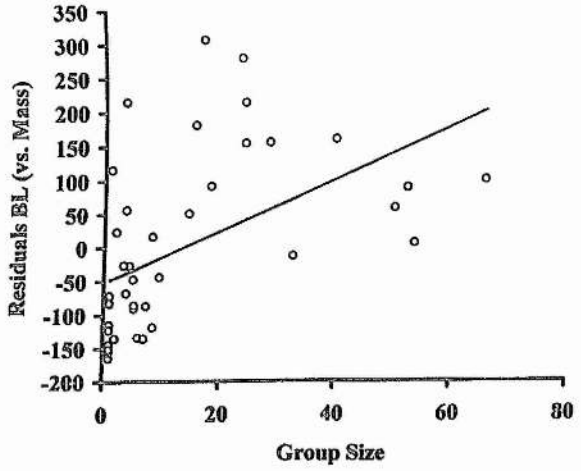
	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* value**	**df**	***p***
BL complex	0.50	0.25	12.94	1, 39	<0.001
CM complex	0.33	0.11	4.9	1, 39	<0.05
LB nucleus	0.59	0.35	20.66	1, 39	<0.0001
Rest of Amygdala	0.44	0.19	9.41	1, 39	<0.01
Amygdala	0.46	0.21	10.6	1, 39	<0.01
Rest of Brain	0.52	0.27	14.37	1, 39	<0.001

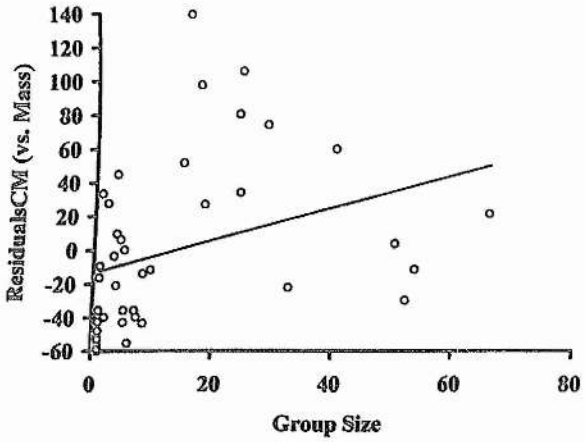
The effects of the volume of a corresponding brain area (for example, the rest of the amygdala for the LB nucleus, the CM complex for the BL complex, the BL complex for the CM and the rest of the brain for the amygdala) were partialled out and all brain areas (except for the amygdala) were significantly correlated with mean group size (see Table 5.5 and Figure 5.3 for scatter plots of significant results).

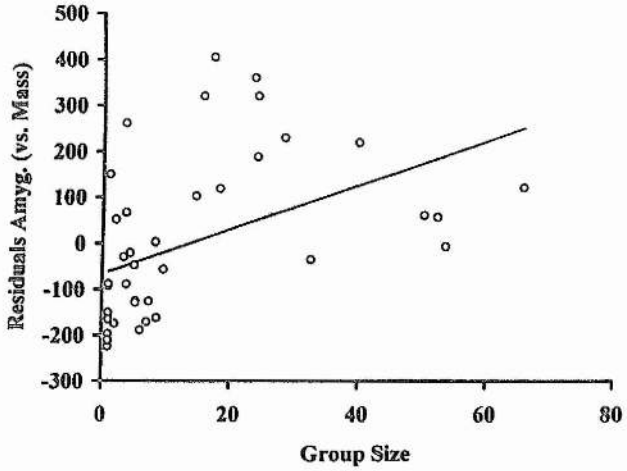
Figure 5.2. Scatterplots displaying the relationship between (a) the residuals of the volume of the LB nucleus (removing the effects of body mass), and mean group size, for strepsirhine and haplorhine primates, (b) the residuals of the volume of the rest of the amygdala (RoA, removing the effects of body mass), and mean group size, (c) the residuals of the volume of the BL complex (removing the effects of body mass), and mean group size, (d) the residuals of the volume of the CM complex (removing the effects of body mass), and mean group size, (e) the residuals of the volume of the amygdala (removing the effects of body mass), and mean group size and (f) the residuals of the volume of the rest of the brain (RoB, removing the effects of body mass) and mean group size. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.






Residuals BL (vs. Mass)
350
300
250
200
150
100
50
0
-50
-100
-150
-200
0
20
40
60
80
Group Size


ResidualsCM (vs. Mass)
140
120
100
80
60
40
20
0
-20
-40
-60
0
20
40
60
80
Group Size


Residuals Amyg. (vs. Mass)
500
400
300
200
100
0
-100
-200
-300
0
20
40
60
80
Group Size

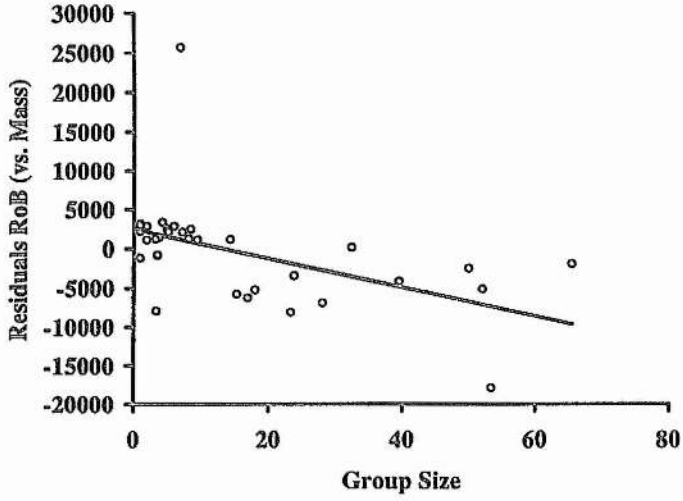
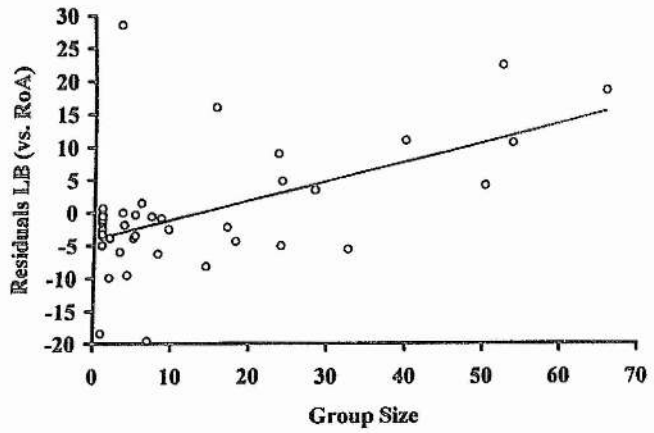
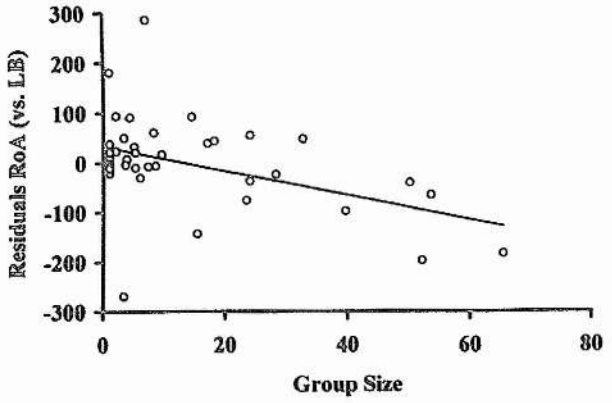
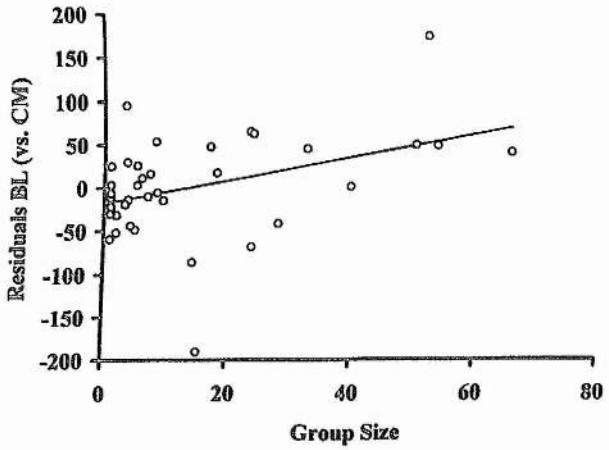

Residuals RoB (vs. Mass)
30000
25000
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
0
20
40
60
80
Group Size

Figure 5.3. Scatterplots displaying the relationships between **(a)** the residuals of the volume of the LB nucleus (removing the effects of the RoA), and mean group size for strepsirhine and haplorhine primates, **(b)** the residuals of the volume of the RoA (removing the effects of the LB nucleus), and mean group size, **(c)** the residuals of the volume of the BL complex (removing the effects of the CM complex), and mean group size, **(d)** the residuals of the volume of the CM complex (removing the effects of the BL complex), and mean group size. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.






Residuals BL (vs. CM)
200
150
100
50
0
-50
-100
-150
-200
0
20
40
60
80
Group Size

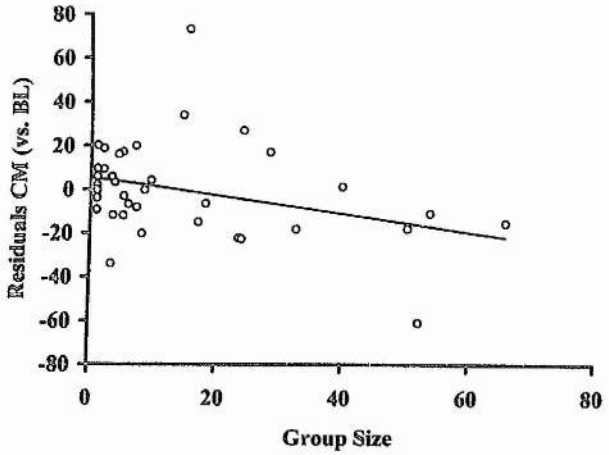

Residuals CM (vs. BL)
80
60
40
20
0
-20
-40
-60
-80
0
20
40
60
80
Group Size

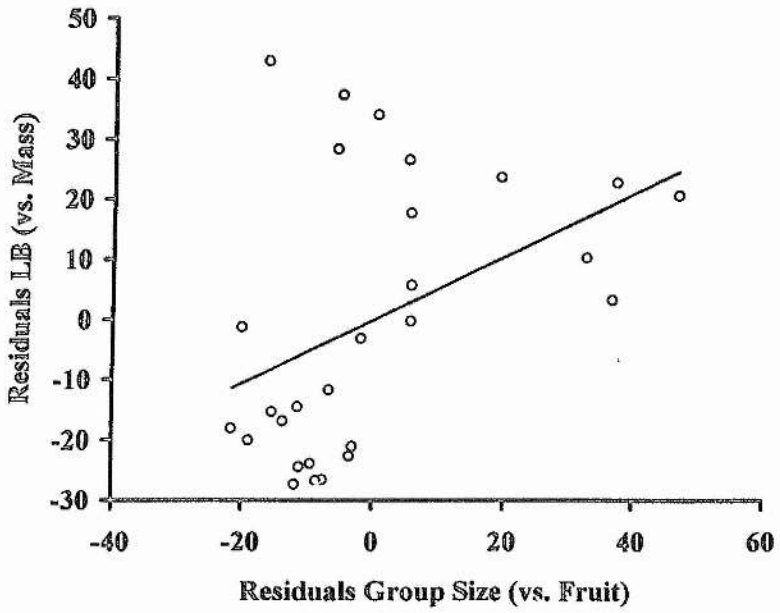
Table 5.5. Regression statistics for relationships between mean group size and volume of brain area (partialling out the influence of volume of the corresponding brain area).

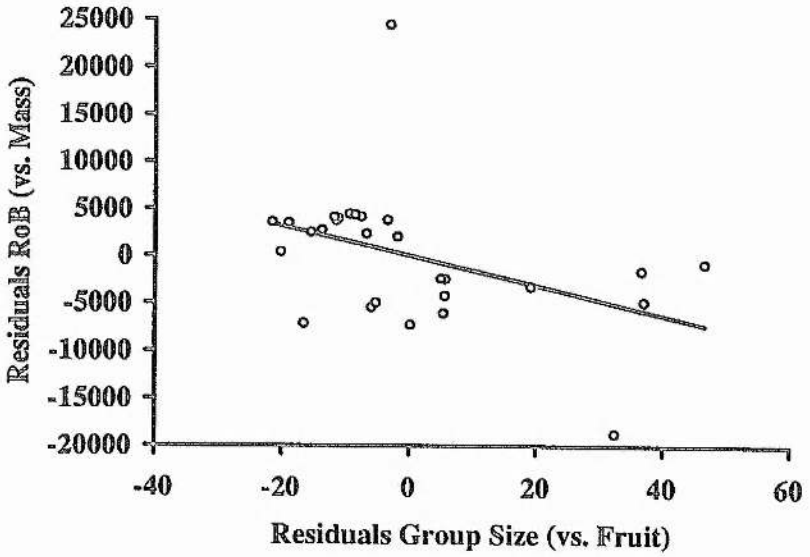
	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL complex (vs. CM complex)	0.4	0.16	7.28	1, 39	<0.01
CM complex (vs. BL complex)	0.34	0.12	5.04	1, 39	<0.05
LB nucleus (vs. Rest of Amygdala)	0.54	0.29	15.82	1, 39	<0.001
Rest of Amygdala (vs. LB nucleus)	0.45	0.2	9.75	1, 39	<0.01
Amygdala (vs. Rest of Brain)	0.10	0.01	0.42	1, 39	0.52
Rest of Brain (vs. Amygdala)	0	0	0	1, 39	1.0

Mean group size may be affected by ecological variables, such as diet and size of home range. The percentage of fruit in the diet may effect social relationships as fruit is a scattered resource which cannot sustain large numbers of individuals (Milton 1988). Primates which eat a high amount of fruit would therefore be more solitary animals. Primate which eat a mainly folivorous diet can eat together, as foliage is plentiful and not clumped. The correlation between mean group size and percentage fruit was not significant ($r^2 = 0.06$, $F(1,26) = 1.62$, $p = 0.21$), but this may have been affected by the low levels of fruit eaten by prosimians. When the possible effects of fruit were removed from mean group size, the residuals significantly correlated with the residuals of LB (vs. mass), $r^2 = 0.19$, $F(1,26) = 5.9$, $p < 0.05$ and the residuals of the rest of the brain (vs. mass), $r^2 = 0.16$, $F(1,26) = 5.11$, $p < 0.05$. There were non-significant correlations between residuals of group size (vs. fruit) and residuals of the following brain areas (vs. mass); BL complex, $r^2 = 0.11$, $p = 0.08$; CM complex, $r^2 = 0.02$, $p = 0.45$; rest of amygdala, $r^2 = 0.07$, $p = 0.17$ and the amygdala, $r^2 = 0.08$, $p = 0.13$. Figure 5.4 displays scatter plots of the significant results.

Mean group size may also be affected by home range size. A larger home range may be required by fruit eaters and to sustain larger groups. There is a significant correlation between home range size and mean group size ($r^2 = 0.3$, $F(1,28) = 11.93$, $p <$

Figure 5.4. Scatterplots displaying the relationships between (a) the residuals of the volume of the LB nucleus (removing the effects of body mass) and the residuals of mean group size (removing the effects of percentage fruit in the diet) for strepsirhine and haplorhine primates, (b) the residuals of the volume of the rest of the brain (removing the effects of body mass) and the residuals of mean group size (removing the effects of percentage fruit in the diet). The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.





0.01), but not between home range size and percentage fruit ($r^2 = 0.04$, $p = 0.4$). When the effect of home range size was removed from mean group size, the residuals were significantly correlated with the residuals of BL complex (vs. mass), $r^2 = 0.15$, $F(1,28) = 4.93$, $p < 0.05$; residuals of the LB nucleus (vs. mass), $r^2 = 0.15$, $F(1,28) = 4.78$, $p < 0.05$ and residuals of the rest of the brain (vs. mass), $r^2 = 0.25$, $F(1,28) = 9.35$, $p < 0.01$. The residuals were not significantly correlated with the residuals of the following brain areas (vs. mass); CM, $r^2 = 0.02$, $p = 0.39$; rest of amygdala, $r^2 = 0.06$, $p = 0.19$ and amygdala, $r^2 = 0.09$, $p = 0.09$. Figure 5.5 displays scatter plots of the significant results.

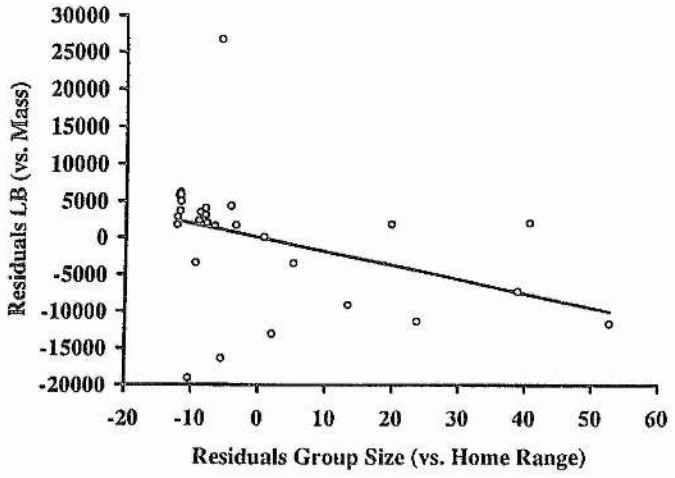
Number of females in a group may provide an indication of male competition and mating opportunities. Linear regressions were performed between the brain areas and number of females in a group. All brain areas were positively correlated with number of females, when controlling for body mass. See Table 5.6 for regression statistics and Figure 5.6 for scatter plots of significant results.

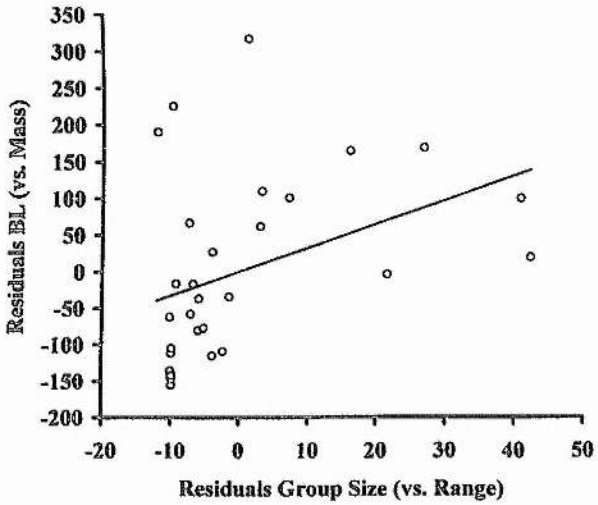
Table 5.6. Regression statistics for relationships between number of females in a group and volume of brain area (partialling out the effects of body mass on the volume of the brain area).

	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex	0.48	0.23	11.35	1, 38	<0.01
CM Complex	0.36	0.13	5.73	1, 38	<0.05
LB Nucleus	0.52	0.27	13.88	1, 38	<0.001
Rest of Amygdala	0.44	0.20	9.25	1, 38	<0.01
Amygdala	0.46	0.21	9.9	1, 38	<0.01
Rest of Brain	0.42	0.17	7.90	1, 38	<0.01

When number of females were regressed against brain area (removing the effects of the corresponding brain area), only the LB nucleus and the rest of the amygdala were

Figure 5.5. Scatterplots displaying the relationships between (a) the residuals of the volume of the LB nucleus (removing the effects of body mass) and the residuals of mean group size (removing the effects of mean home range size), for strepsirhine and haplorhine primates, (b) the residuals of the volume of the BL complex (removing the effects of body mass) and the residuals of mean group size (removing the effects of mean home range size), and (c) the residuals of the volume of the RoB (removing the effects of body mass) and the residuals of mean group size (removing the effects of mean home range size). The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.





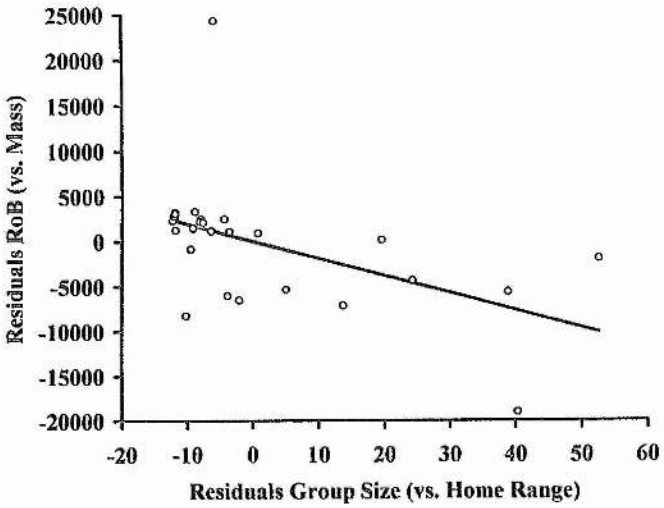
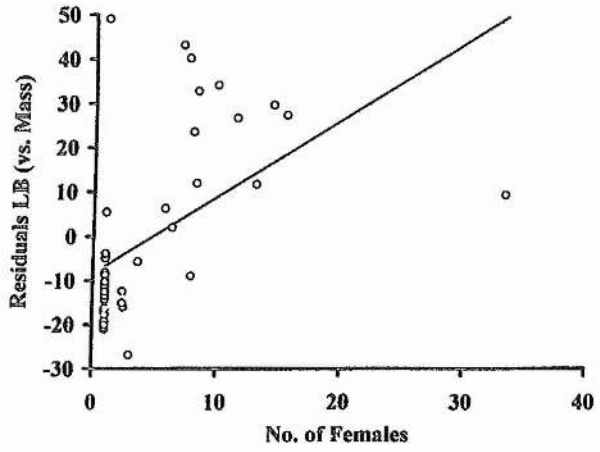
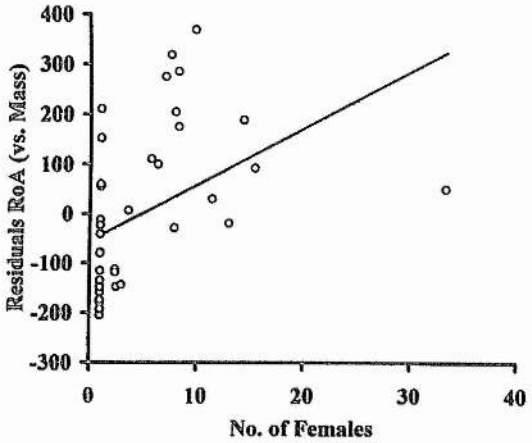
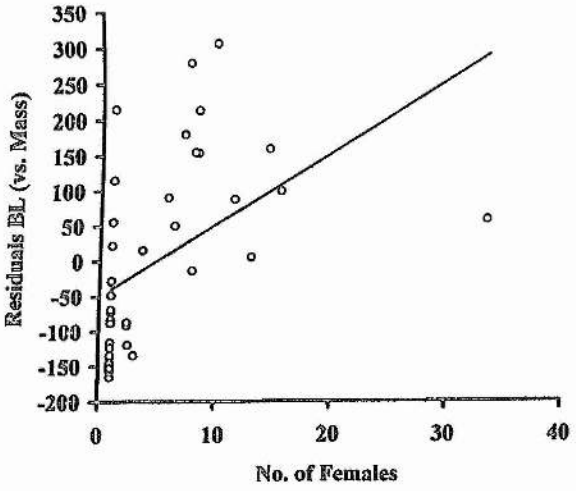
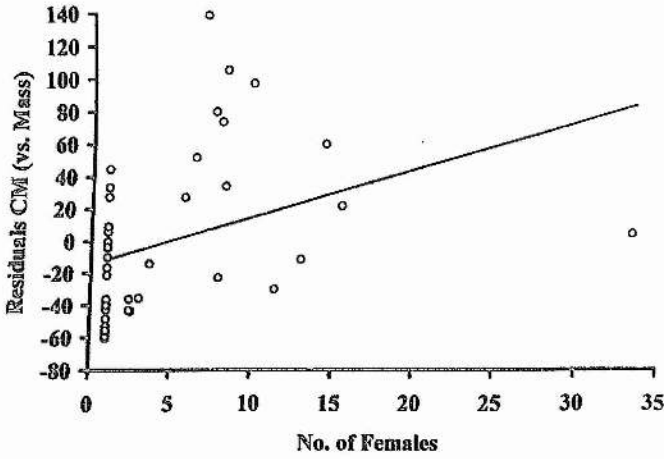


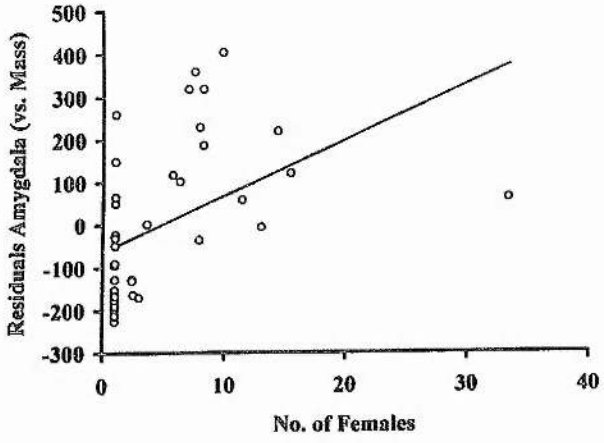
Figure 5.6. Scatterplots displaying the relationship between (a) the residuals of the volume of the LB nucleus (removing the effects of body mass), and number of females in a group, for strepsirhine and haplorhine primates, (b) the residuals of the volume of the rest of the amygdala (RoA, removing the effects of body mass), and number of females in a group, (c) the residuals of the volume of the BL complex (removing the effects of body mass), and number of females in a group, (d) the residuals of the volume of the CM complex (removing the effects of body mass), and number of females in a group, (e) the residuals of the volume of the amygdala (removing the effects of body mass), and number of females in a group and (f) the residuals of the volume of the rest of the brain (RoB, removing the effects of body mass) and number of females in a group. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.

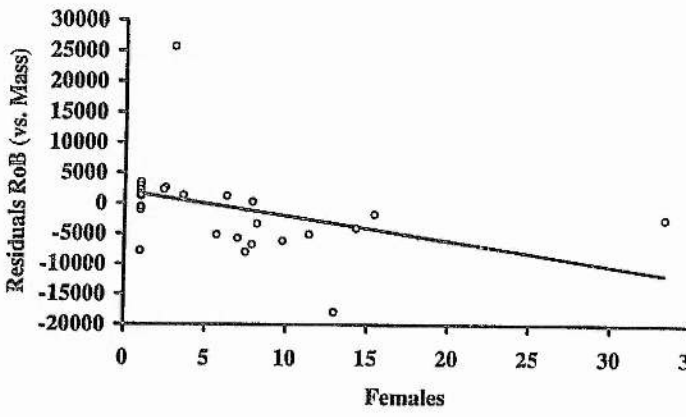





Residuals BL (vs. Mass)
350
300
250
200
150
100
50
0
-50
-100
-150
-200
0
10
20
30
40
No. of Females


Residuals CM (vs. Mass)
140
120
100
80
60
40
20
0
-20
-40
-60
-80
0
5
10
15
20
25
30
35
No. of Females


Residuals Amygdala (vs. Mass)
500
400
300
200
100
0
-100
-200
-300
0
10
20
30
40
No. of Females


Residuals RoB (vs. Mass)
30000
25000
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
0
5
10
15
20
25
30
Females

significantly correlated (see Table 5.7 for regression statistics). Scatter plots displaying the significant results are in Figures 5.7.

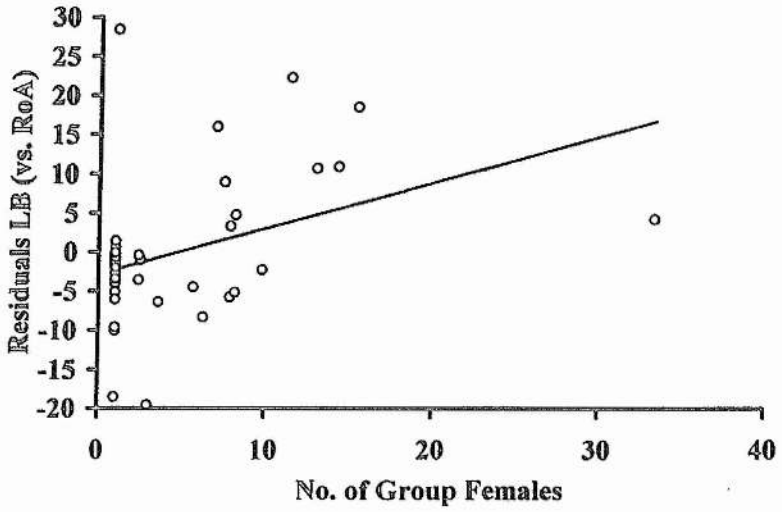
Table 5.7. Regression statistics for relationships between number of females in a group and volume of brain area (controlling for effects of volume of the corresponding brain area).

	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex (vs. CM Complex)	0.28	0.08	3.23	1, 38	0.08
CM Complex (vs. BL Complex)	0.23	0.05	2.14	1, 38	0.15
LB Nucleus (vs. Rest of Amygdala)	0.39	0.15	6.62	1, 38	<0.01
Rest of Amygdala (vs. LB Nucleus)	0.31	0.10	4.07	1, 38	<0.05
Amygdala (vs. Rest of Brain)	0.03	0.001	0.04	1, 38	0.85
Rest of Brain (vs. Amygdala)	0.06	0.003	0.15	1, 38	0.7

Percentage fruit in the diet may effect the number of females in the group in similar ways to the effect on group size, although the relationship is not significant ($r^2 = 0.02$, $p = 0.5$). The effects of percentage fruit in diet were removed from number of females and the residuals were significantly correlated only with the residuals of the LB nucleus (vs. mass), $r^2 = 0.15$, $F(1,26) = 4.55$, $p < 0.05$. The residuals were not significantly correlated with the residuals (vs. mass) of the following brain areas; BL complex, $r^2 = 0.13$, $p = 0.06$; CM complex, $r^2 = 0.06$, $p = 0.23$; rest of amygdala, $r^2 = 0.11$, $p = 0.09$, amygdala, $r^2 = 0.11$, $p = 0.08$ and rest of the brain (vs. mass), $r^2 = 0.32$, $F(1,26) = 3.02$, $p = 0.09$. The significant results are displayed as scatter plots in Figure 5.8.

The effects of home range size were also removed from number of females, as there is a significant relationship between range and number of females ($r^2 = 0.26$, $F(1,27) = 9.56$, $p < 0.01$). The residuals were significantly correlated with the residuals of BL complex (vs. mass), $r^2 = 0.18$, $F(1,27) = 5.76$, $p < 0.05$; LB nucleus (vs. mass), $r^2 = 0.15$, $F(1,27) = 4.87$, $p < 0.05$; rest of amygdala (vs. mass), $r^2 = 0.14$, $F(1,27) = 4.29$, p

Figure 5.7. Scatterplots displaying the relationships between (a) the residuals of the volume of the LB nucleus (removing the effects of the RoA), and number of females in a group, for strepsirhine and haplorhine primates and (b) the residuals of the volume of the RoA (removing the effects of the LB nucleus), and number of females in a group. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.



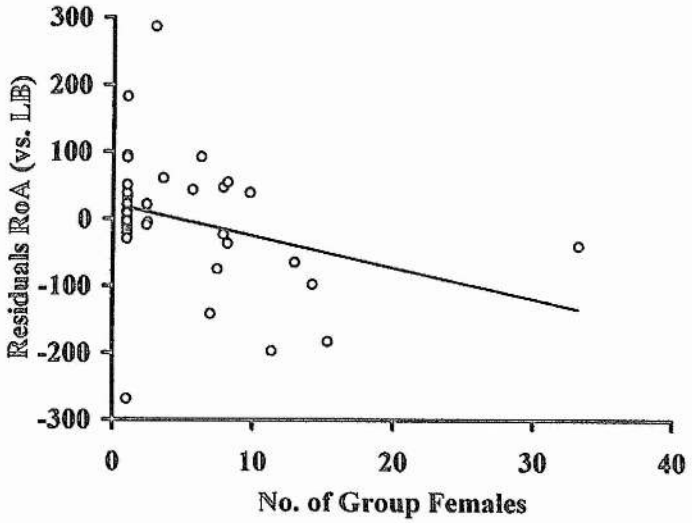
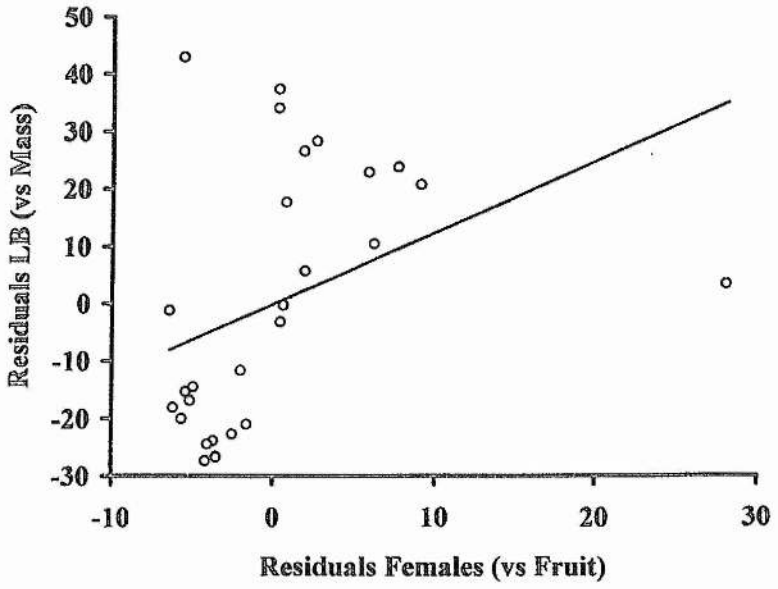


Figure 5.8. Scatterplots displaying the relationships between the residuals of the volume of the LB nucleus (removing the effects of body mass) and the residuals of number of females in a group (removing the effects of percentage fruit in the diet) for strepsirhine and haplorhine primates. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.



< 0.05, amygdala (vs. mass), $r^2 = 0.15$, $F(1,27) = 4.58$, $p < 0.05$ and the rest of the brain (vs. mass), $r^2 = 0.23$, $F(1,27) = 8.14$, $p < 0.01$. The residuals of CM (vs. mass) were not significantly correlated with the residuals of number of females (vs. home range), $r^2 = 0.06$, $p = 0.21$. Scatter plots of the significant results are displayed in Figure 5.9.

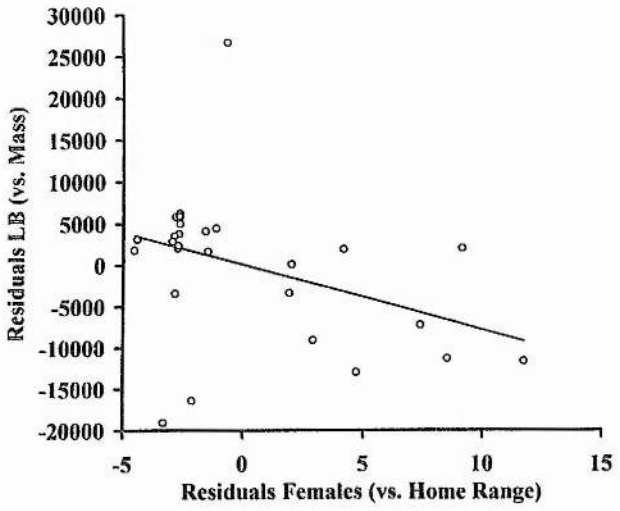
A final measure of social complexity was proposed; percentage time spent grooming. When percentage time grooming was regressed against brain area (removing the effects of body mass), only the residuals of the LB nucleus were significantly correlated (see Table 5.8 and Figure 5.10).

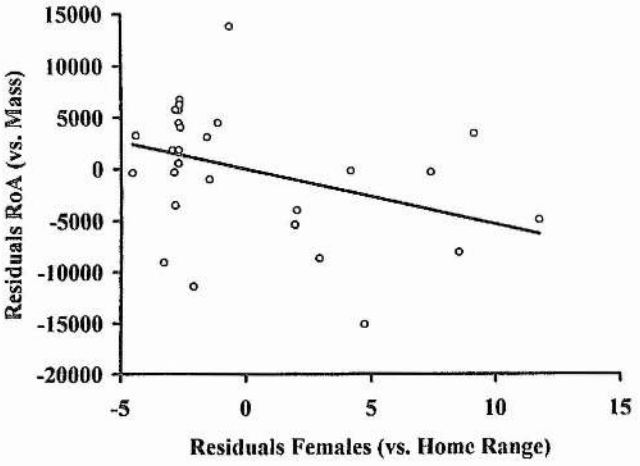
Table 5.8. Regression statistics for relationships between percentage time spent grooming and volume of brain area (controlling for effect of body mass on brain area volume).

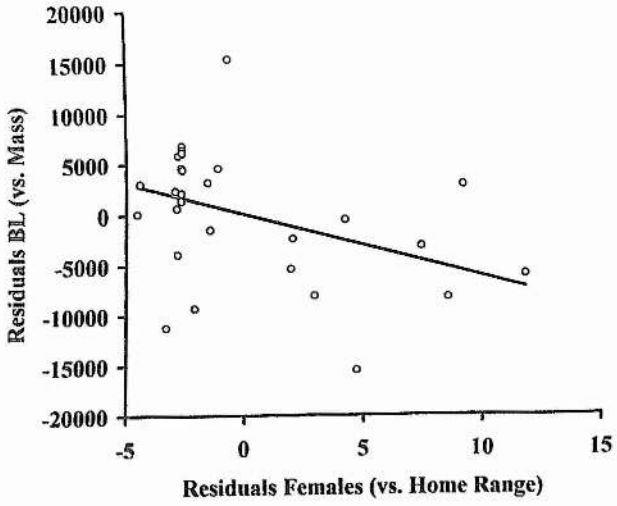
	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex	0.46	0.21	3.76	1, 14	0.07
CM Complex	0.31	0.10	1.47	1, 14	0.25
LB Nucleus	0.56	0.31	6.37	1, 14	<0.05
Rest of Amygdala	0.41	0.17	2.77	1, 14	0.12
Amygdala	0.43	0.19	3.25	1, 14	0.09
Rest of Brain	0.43	0.18	3.13	1, 14	0.09

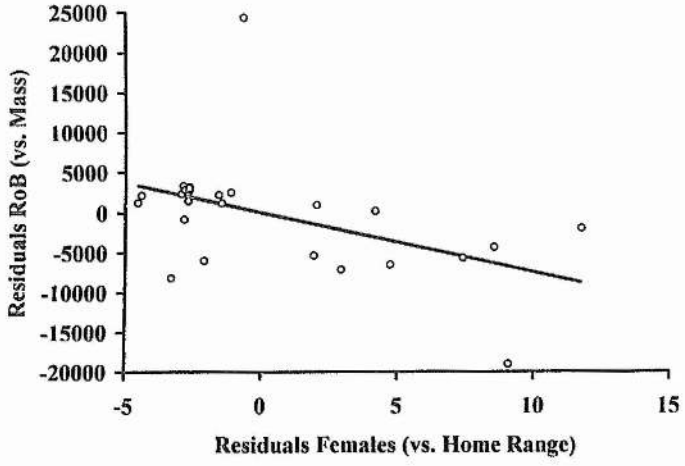
When percentage grooming time was regressed against the residuals of brain area (vs. corresponding brain area), there were significant correlations with the LB nucleus and the rest of the amygdala (see Table 5.9 and scatter plots of significant results displayed in Figure 5.11).

Figure 5.9. Scatterplots displaying the relationships between **(a)** the residuals of the volume of the LB nucleus (removing the effects of body mass) and the residuals of the number of females in a group (removing the effects of mean home range size) for strepsirhine and haplorhine primates, **(b)** the residuals of the volume of the RoA (removing the effects of body mass) and the residuals of the number of females in a group (removing the effects of mean home range size), **(c)** the residuals of the volume of the BL complex (removing the effects of body mass) and the residuals of the number of females in a group (removing the effects of mean home range size), **(d)** the residuals of the volume of the RoB (removing the effects of body mass) and the residuals of the number of females in a group (removing the effects of mean home range size) and **(e)** the residuals of the volume of the amygdala (removing the effects of body mass) and the residuals of the number of females in a group (removing the effects of mean home range size). The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.






Residuals BL (vs. Mass)
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
-5
0
5
10
15
Residuals Females (vs. Home Range)


Residuals RoB (vs. Mass)
25000
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
-5
0
5
10
15
Residuals Females (vs. Home Range)

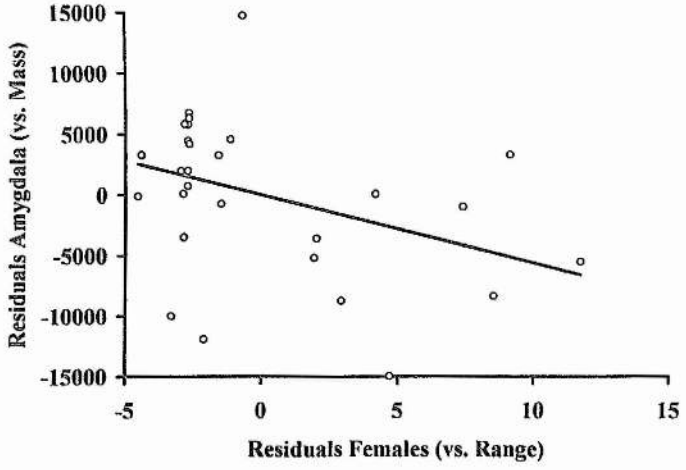

Residuals Amygdala (vs. Mass)
15000
10000
5000
0
-5000
-10000
-15000
-5
0
5
10
15
Residuals Females (vs. Range)

Figure 5.10. Scatterplot displaying the relationships between the residuals of the LB nucleus (removing the effects of body mass) and percentage time spent grooming, for strepsirhine and haplorhine primates. The dots represent individual primate species and the line on the scatter-plot is a best-fit regression line.

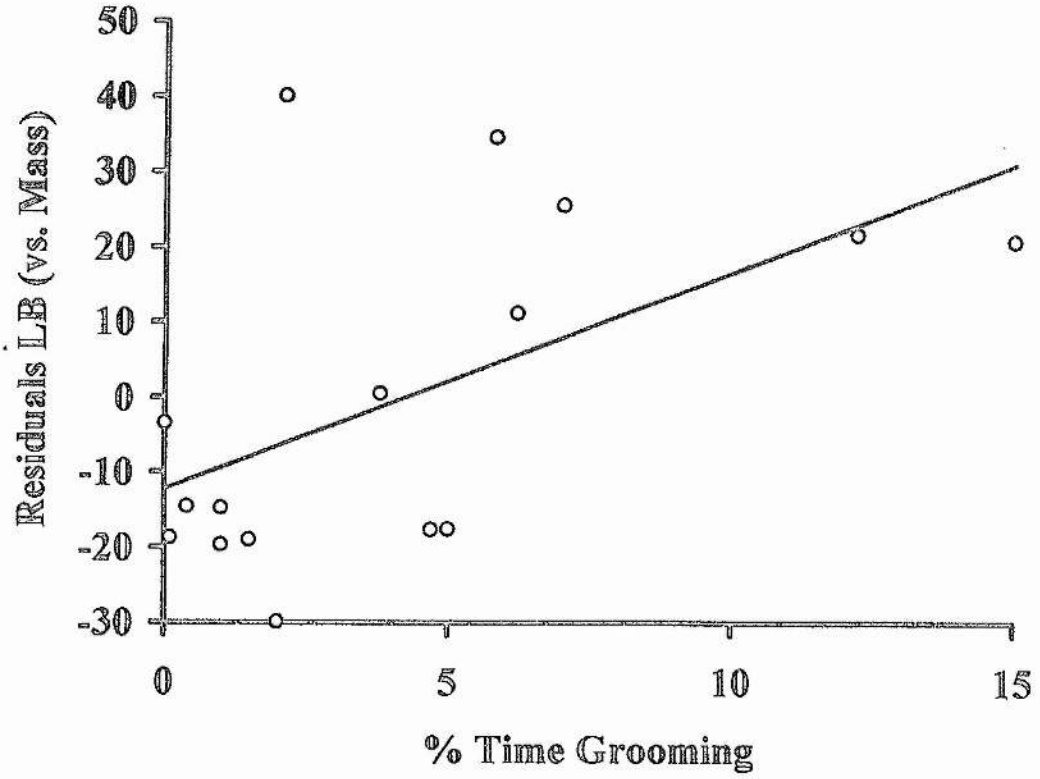
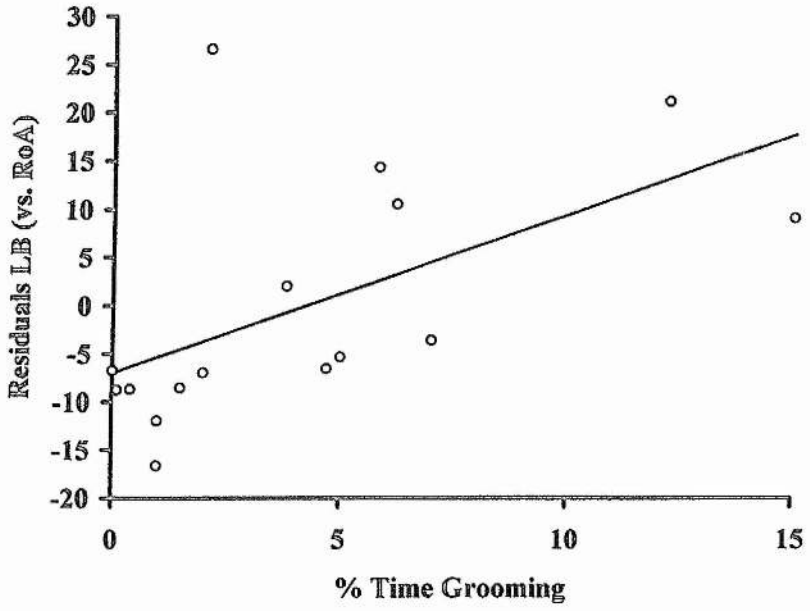


Figure 5.11. Scatterplots displaying the relationships between (**a**) the residuals of the volume of the LB nucleus (removing the effects of the RoA) and percentage time spent grooming, for strepsirhine and haplorhine primates and (**b**) the residuals of the volume of the RoA (removing the effects of the LB nucleus) and percentage time spent grooming. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.



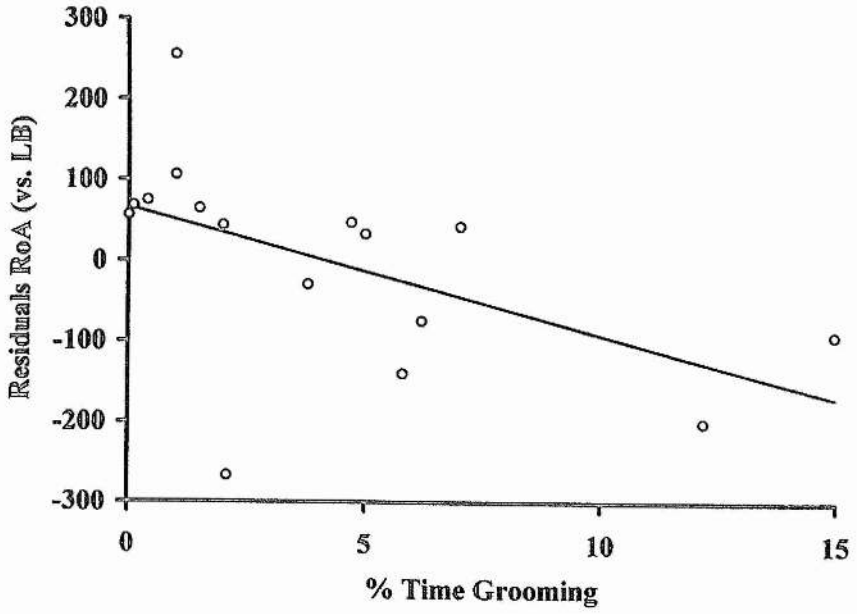


Table 5.9. Regression statistics for relationships between percentage time spent grooming and volume of brain area (controlling for effects of volume of corresponding brain area).

	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex (vs. CM Complex)	0.19	0.04	0.55	1, 14	0.47
CM Complex (vs. BL Complex)	0.18	0.03	0.46	1, 14	0.51
LB Nucleus (vs. Rest of Amygdala)	0.57	0.32	6.60	1, 14	<0.05
Rest of Amygdala (vs. LB Nucleus)	0.53	0.28	5.54	1, 14	<0.05
Amygdala (vs. Rest of Brain)	0.09	0.01	0.12	1, 14	0.73
Rest of Brain (vs. Amygdala)	0.13	0.02	0.24	1, 14	0.63

Percentage fruit in the diet may affect percentage time grooming, as finding and eating fruit is time consuming, reducing the possible time which can be spent on grooming. The relationship between fruit and grooming, however is non-significant, $r^2 = 0.44$, $p = 0.13$. None of the residuals of brain area (vs. mass) were significantly correlated with the residuals of grooming (vs. percentage fruit in diet); BL complex, $r^2 = 0.03$, $p = 0.6$; CM complex, $r^2 = 0$, $p = 0.99$, LB nucleus, $r^2 = 0.07$, $p = 0.37$; rest of amygdala, $r^2 = 0.008$, $p = 0.77$; amygdala, $r^2 = 0.01$, $p = 0.7$ and rest of brain, $r^2 = 0.02$, $p = 0.61$.

Grooming may also be affected by home range size, as a widely dispersed food source requires longer to find and process food. The relationship between grooming and range, however, was non-significant; $r^2 = 0.02$, $p = 0.61$. When the affects of home range size are removed from percentage time grooming, the residuals do not correlate with any of the residuals of brain area (vs. mass); BL complex, $r^2 = 0.12$, $p = 0.22$; CM complex, $r^2 = 0.009$, $p = 0.73$, LB nucleus, $r^2 = 0.17$, $p = 0.15$; rest of amygdala, $r^2 = 0.09$, $p = 0.31$; amygdala, $r^2 = 0.08$, $p = 0.32$ and rest of brain, $r^2 = 0.13$, $p = 0.2$.

5.3.2 Ecology

There was an overall effect of diet on the size of the LB nucleus, $F(2,41) = 3.28$, $p < 0.05$. Frugivores (PLSD, $p < 0.05$) and folivores (PLSD, $p < 0.05$) have a larger LB

nucleus than insectivores (see Figure 5.12). There was no difference between the two groups of plant-eating primates (PLSD, $p = 0.79$). There was no overall effect of diet on the BL complex, $F(2,41) = 0.34$, $p = 0.71$, on the CM complex, $F(2,41) = 0.34$, $p = 0.68$ or on the amygdala, $F(2,40) = 2.36$, $p = 0.11$.

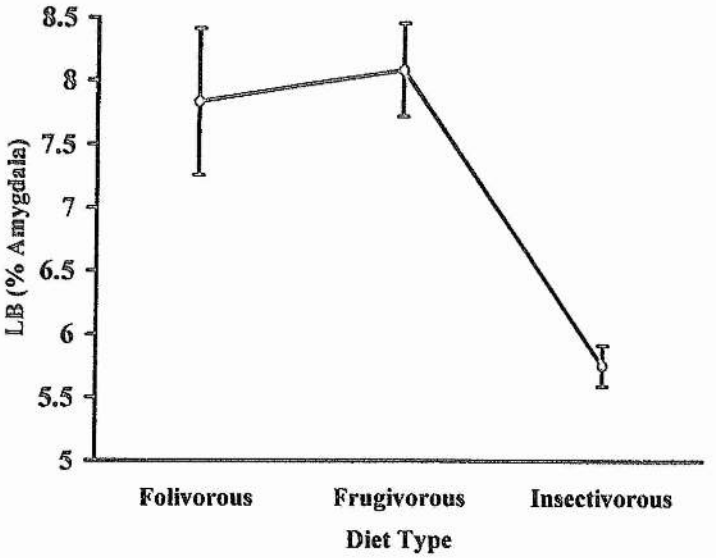
Relationships between the ecological variables and the seven brain regions were also analysed further. Two measures of ecological complexity were analysed; home range size and percentage fruit in the diet. When home range size was regressed against volume of brain area (removing the effects of body mass), the residuals of all areas (except the rest of the brain) were significantly correlated (see Table 5.10 and scatter plots displayed in Figure 5.13) with home range size.

Table 5.10. Regression statistics for relationships between home range size (km2) and volume of brain area (controlling for the effects of body mass on brain area volume).

	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex	0.51	0.26	10.09	1, 28	< 0.01
CM Complex	0.7	0.49	26.76	1, 28	< 0.00001
LB Nucleus	0.54	0.29	11.47	1, 28	<0.01
Rest of Amygdala	0.58	0.33	14.08	1, 28	< 0.001
Amygdala	0.58	0.34	14.14	1, 28	< 0.001
Rest of Brain	0.28	0.08	2.47	1, 28	0.13

When home range size was regressed against the residuals of volume of brain area (vs. corresponding brain area), significant correlations were found with the BL complex and the CM complex (see Table 5.11 and scatter plots displayed in Figure 5.14).

Figure 5.12. (a) Graph depicting the differences between the mean percentage size (+/- SEM) of the LB nucleus (as a percentage of the amygdala) for 44 primate species (strepsirhines and haplorhines), where each species has been grouped dependent on diet (folivorous, frugivorous or insectivorous). (b) Graph depicting the differences between the mean percentage size (+/- SEM) of the amygdala (as a percentage of the brain), where each species has been group dependent on diet.



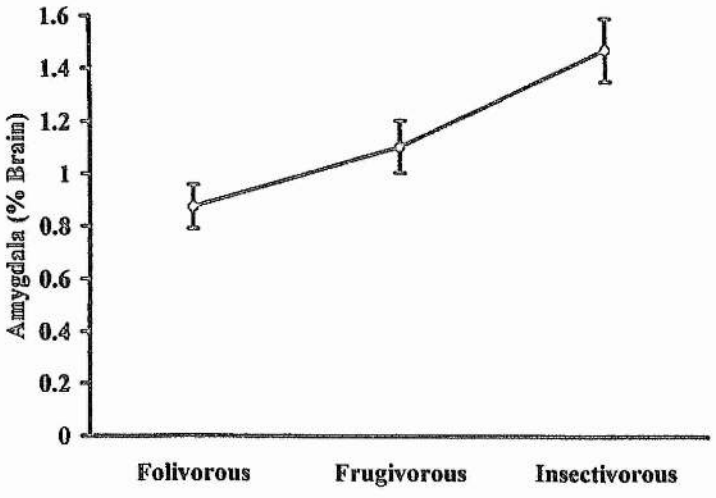
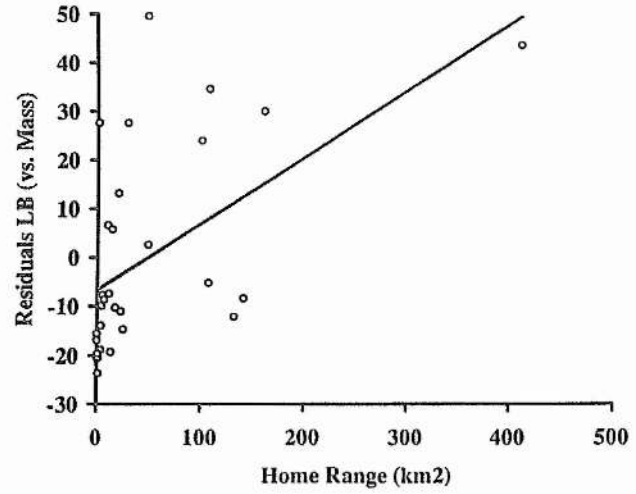
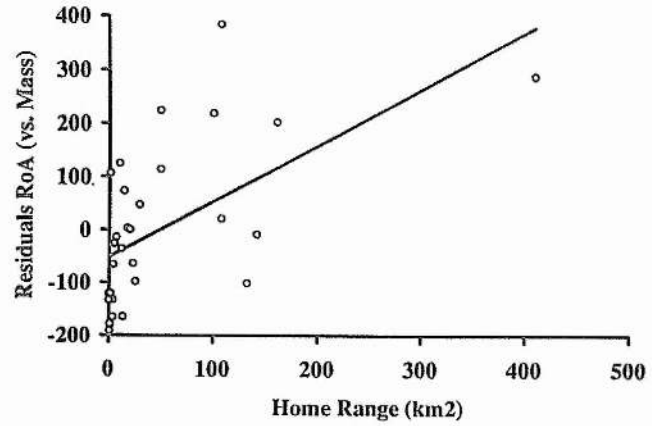
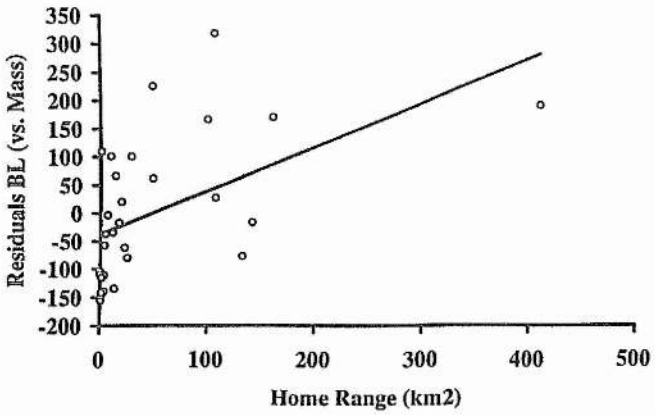
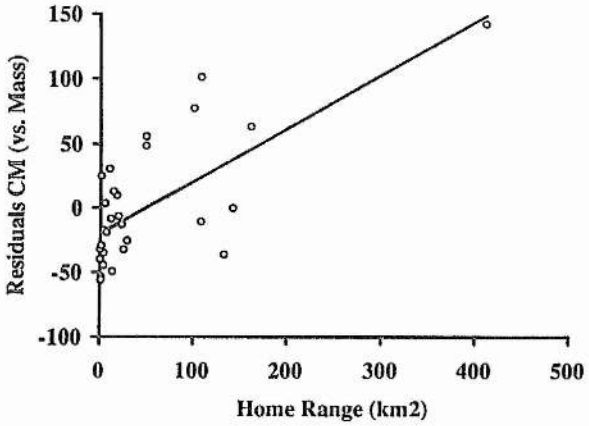


Figure 5.13. Scatterplot of **(a)** the residuals of the volume of the LB nucleus (removing the effects of body mass) and mean home range size, for strepsirhine and haplorhine primates, **(b)** the residuals of the volume of the rest of the amygdala (removing the effects of body mass) and mean home range size. **(c)** the residuals of the volume of the BL complex (removing the effects of body mass) and mean home range size. **(d)** the residuals of the volume of the CM complex (removing the effects of body mass) and mean home range size and **(e)** the residuals of the volume of the amygdala (removing the effects of body mass) and mean home range size. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.






Residuals BL (vs. Mass)
350
300
250
200
150
100
50
0
-50
-100
-150
-200
0
100
200
300
400
500
Home Range (km2)


Residuals CM (vs. Mass)
150
100
50
0
-50
-100
0
100
200
300
400
500
Home Range (km2)

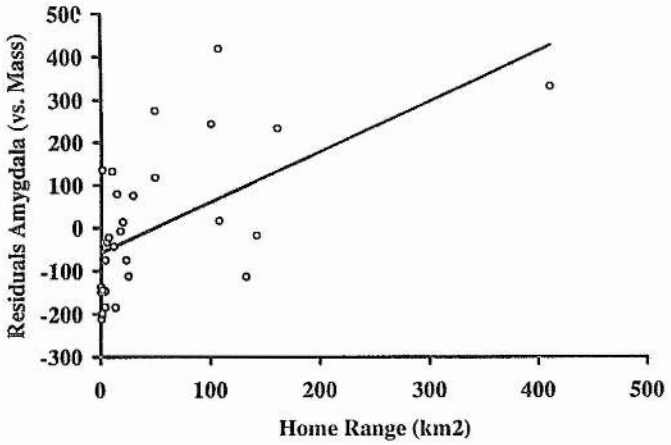
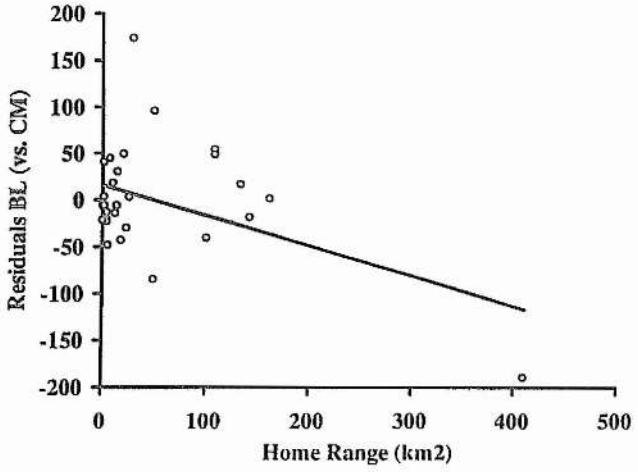

Residuals Amygdala (vs. Mass)
500
400
300
200
100
0
-100
-200
-300
0
100
200
300
400
500
Home Range (km2)

Figure 5.14. Scatterplots displaying the relationships between **(a)** the residuals of the volume of the BL compex (removing the effects of the CM complex) and mean home range size, for strepserhine and haplorhine species, **(b)** the residuals of the volume of the CM compex (removing the effects of the BL complex) and mean home range size. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.



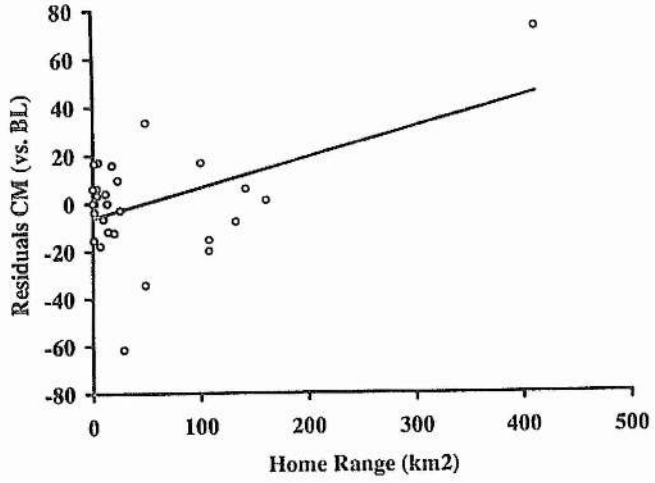


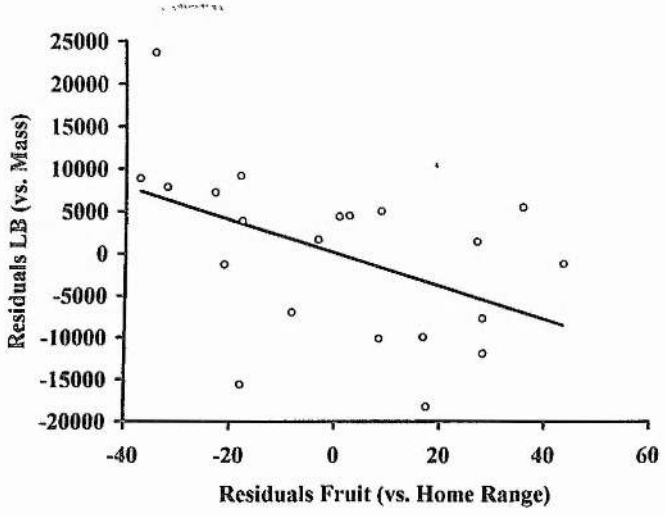
Table 5.11. Regression statistics for relationships between home range size and volume of brain area (controlling for the effects of the volume of the corresponding brain area).

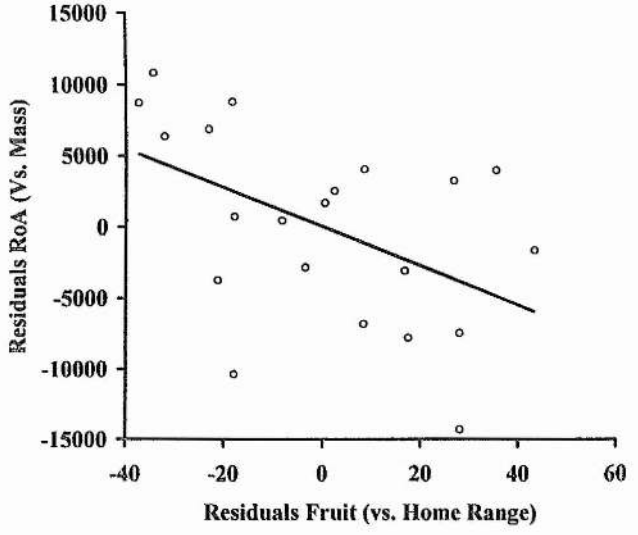
	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex (vs. CM Complex)	0.45	0.2	7.13	1, 28	< 0.01
CM Complex (vs., BL Complex)	0.47	0.22	8.09	1, 28	< 0.01
LB Nucleus (vs. Rest of Amygdala)	0.29	0.09	2.64	1, 28	0.11
Rest of Amygdala (vs. LB Nucleus)	0.26	0.07	2.05	1, 28	0.16
Amygdala (vs. Rest of Brain)	0.32	0.10	3.23	1, 28	0.08
Rest of Brain (vs. Amygdala)	0.32	0.10	3.23	1, 28	0.08

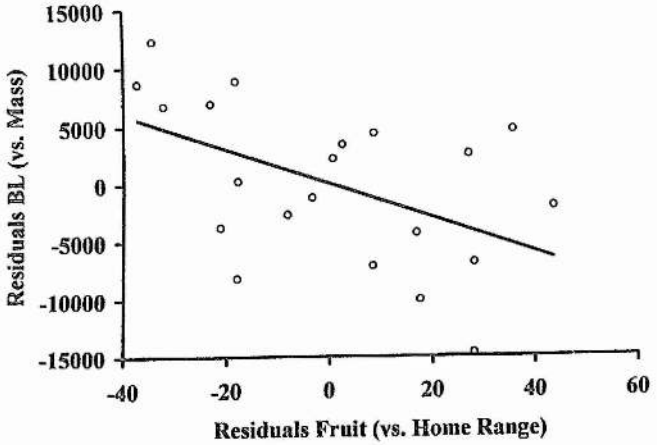
Percentage fruit in the diet may have an effect on home range size (and visa versa), as fruit is usually widely dispersed. The effects may be hidden, however as there is a non-significant correlation between percentage fruit and home range size ($r^2 = 0.04$, $p = 0.4$). The effects of percentage fruit were removed from home range size and the residuals correlated with the residuals of brain area (vs. mass). All residuals of brain areas were significantly correlated with the residuals of home range size (vs. fruit), rest of brain, $r^2 = 0.25$, $F(1,19) = 6.49$, $p < 0.05$; BL complex, $r^2 = 0.27$, $F(1,19) = 6.95$, $p < 0.05$; LB nucleus, $r^2 = 0.23$, $F(1,19) = 5.71$, $p < 0.05$; rest of amygdala, $r^2 = 0.24$, $F(1,19) = 6.03$, $p < 0.05$ and amygdala, $r^2 = 0.37$, $F(1,19) = 11.28$, $p < 0.01$, except the CM complex, $r^2 = 0.16$, $p = 0.07$. Scatter plots of significant results are displayed in Figure 5.15.

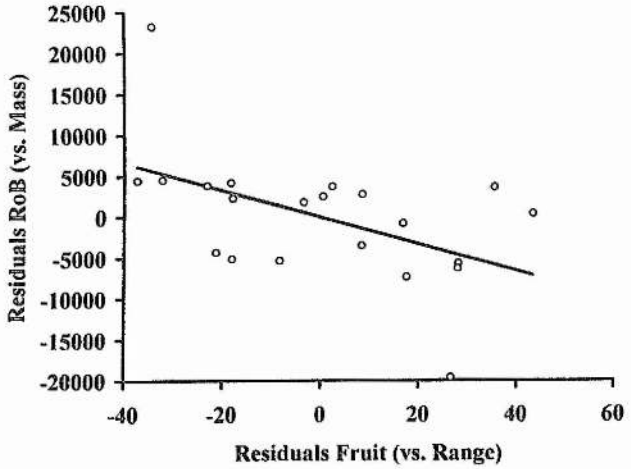
A second measure of ecology used was percentage fruit in the diet. As stated previously, fruit is a scarce resource that requires knowledge of the location of the best fruiting trees, when they are ripe and whether novel fruits are edible in times of need. The higher the percentage of fruit in a diet, the greater the reliance on complex cognitive processes (Milton 1988). When percentage fruit was regressed against volume of brain area (removing the effects of body mass), all areas, except the rest of the brain, were significantly correlated with percentage fruit (see Table 5.12 and scatter plots displayed in Figure 5.16).

Figure 5.15. Scatterplots displaying the relationships between (a) the residuals of the volume of the LB nucleus (removing the effects of body mass) and the residuals of mean home range size (removing the effects of percentage fruit in the diet) for strepsirhine and haplorhine primates, (b) the residuals of the volume of the RoA (removing the effects of body mass) and the residuals of mean home range size (removing the effects of percentage fruit in the diet), (c) the residuals of the volume of the BL complex (removing the effects of body mass) and the residuals of mean home range size (removing the effects of percentage fruit in the diet), (d) the residuals of the volume of the CM complex (removing the effects of body mass) and the residuals of mean home range size (removing the effects of percentage fruit in the diet) and (e) the residuals of the volume of the amygdala (removing the effects of body mass) and the residuals of mean home range size (removing the effects of percentage fruit in the diet). The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.






Residuals BL (vs. Mass)
15000
10000
5000
0
-5000
-10000
-15000
-40
-20
0
20
40
60
Residuals Fruit (vs. Home Range)


Residuals RoB (vs. Mass)
25000
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
-40
-20
0
20
40
60
Residuals Fruit (vs. Range)

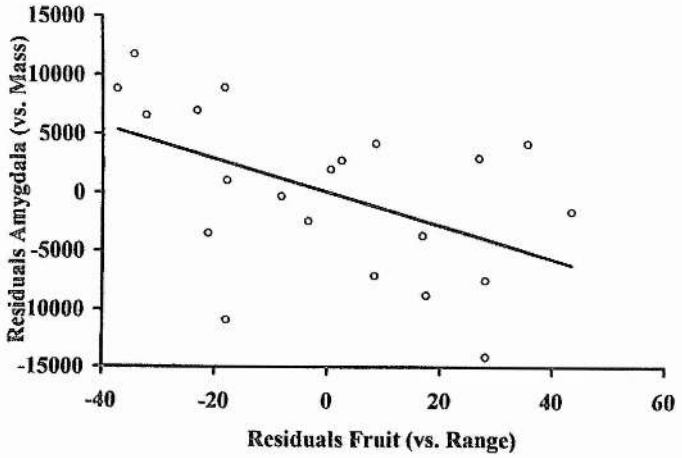
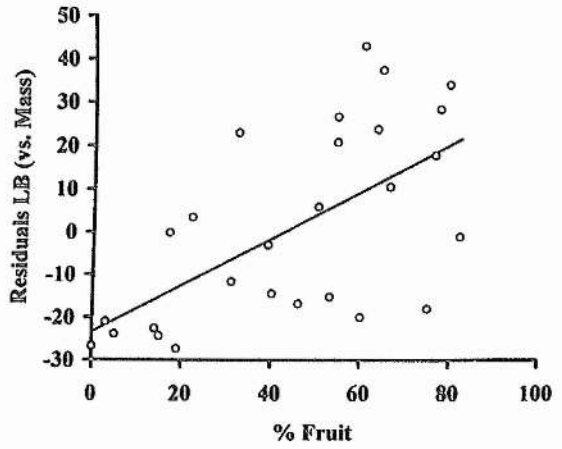
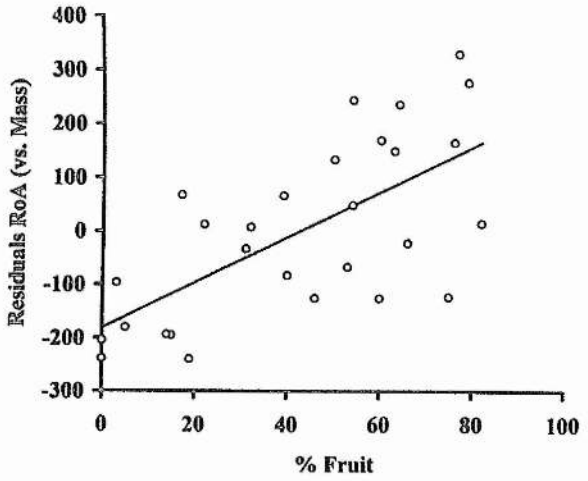
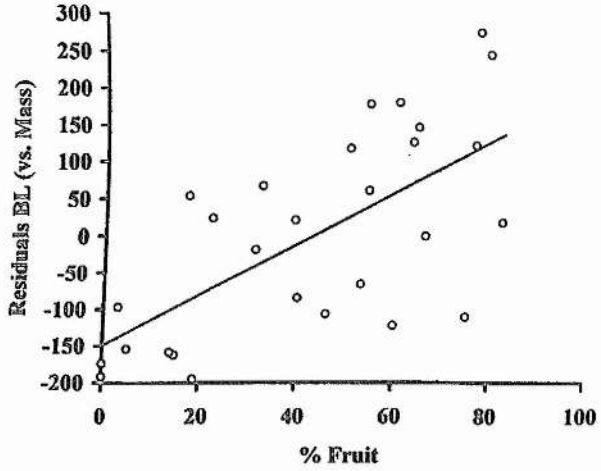
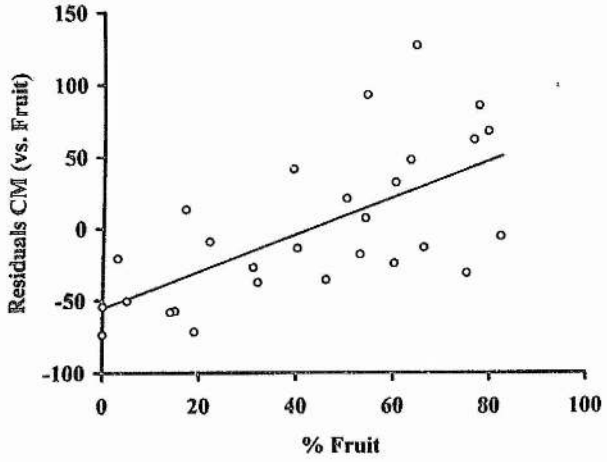

Residuals Amygdala (vs. Mass)
15000
10000
5000
0
-5000
-10000
-15000
-40
-20
0
20
40
60
Residuals Fruit (vs. Range)

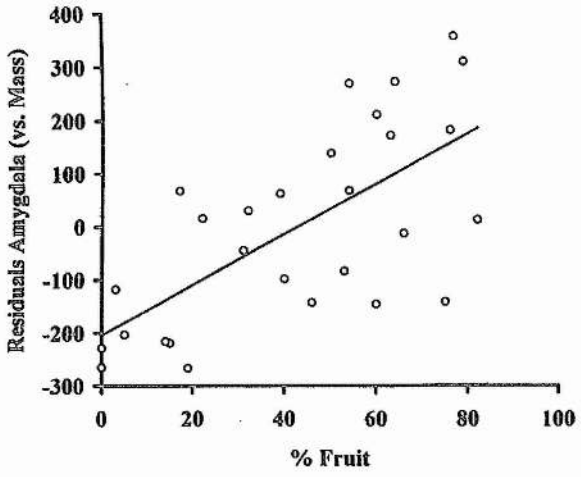
Figure 5.16. Scatterplots displaying the relationships between (a) the residuals of the volume of the LB nucleus (removing the effects of body mass) and percentage fruit in the diet, for strepsirhine and haplorhine primates, (b) the residuals of the volume of the rest of the amygdala (RoA, removing the effects of body mass), and percentage fruit in the diet, (c) the residuals of the volume of the BL complex (removing the effects of body mass), and number of females in a group, (d) the residuals of the volume of the CM complex (removing the effects of body mass), and percentage fruit in the diet and (e) the residuals of the volume of the amygdala (removing the effects of body mass), and percentage fruit in the diet. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.






Residuals BL (vs. Mass)
300
250
200
150
100
50
0
-50
-100
-150
-200
0
20
40
60
80
100
% Fruit


Residuals CM (vs. Fruit)
150
100
50
0
-50
-100
0
20
40
60
80
100
% Fruit


Residuals Amygdala (vs. Mass)
400
300
200
100
0
-100
-200
-300
0
20
40
60
80
100
% Fruit

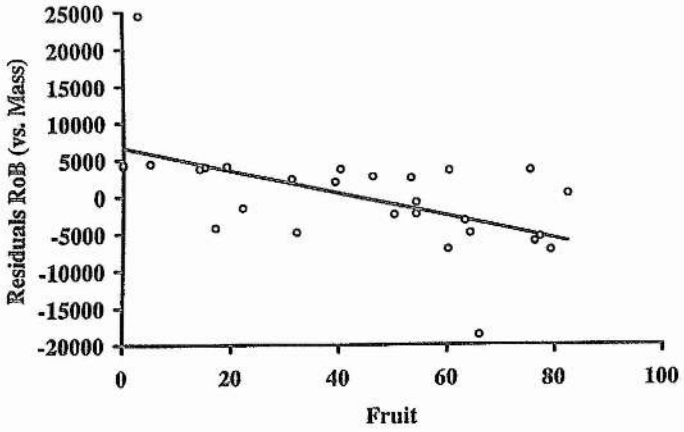

Residuals RoB (vs. Mass)
25000
20000
15000
10000
5000
0
-5000
-10000
-15000
-20000
0
20
40
60
80
100
Fruit

Table 5.12. Regression statistics for relationships between percentage fruit in diet and volume of brain area (controlling for the effects of body mass on volume of brain area).

	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex	0.66	0.44	20.42	1, 26	<0.0001
CM Complex	0.65	0.42	18.80	1, 26	<0.001
LB Nucleus	0.64	0.41	18.11	1, 26	<0.001
Rest of Amygdala	0.67	0.45	21.48	1, 26	<0.00001
Amygdala	0.67	0.45	21.69	1, 26	<0.00001
Rest of Brain	0.57	0.32	12.37	1, 26	<0.01

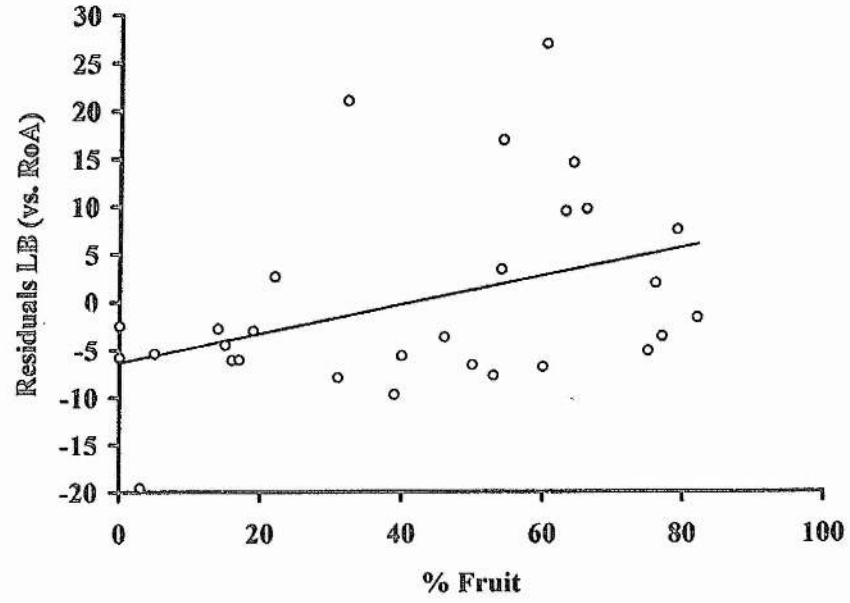
When percentage fruit in diet was regressed against volume of brain area (removing the effects of corresponding brain area), only the residuals of LB nucleus and the rest of the amygdala were significantly correlated (see table 5.13 and scatter plots displayed in Figure 5.17).

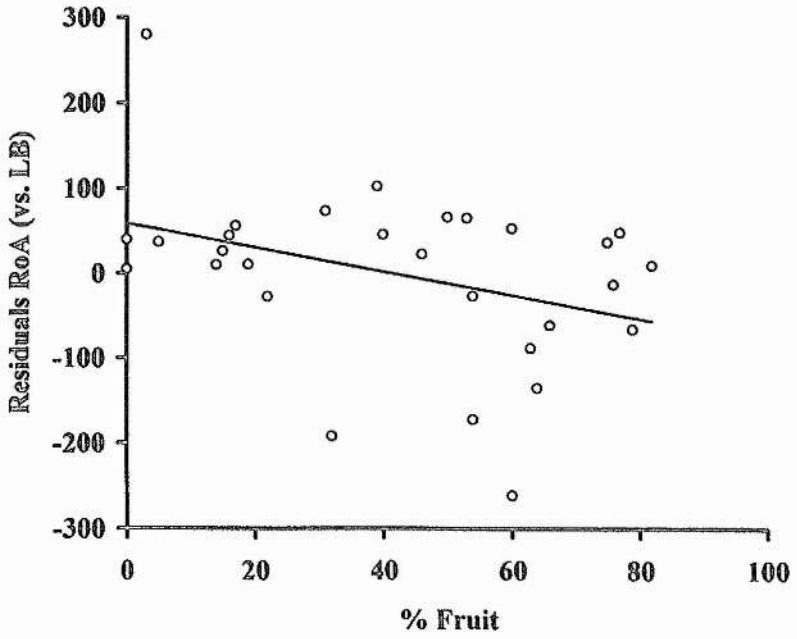
Table 5.13. Regression statistics for relationships between percentage fruit in diet and volume of brain area (controlling for the effects of volume of corresponding brain area).

	Correlation		ANOVA		
Brain Area	**Multiple *R***	***R* Square**	***F* Value**	**df**	***p***
BL Complex (vs. CM Complex)	0.008	0.00007	0.002	1, 27	0.97
CM Complex (vs. BL Complex)	0.008	0.00007	0.002	1, 27	0.97
LB Nucleus (vs. Rest of Amygdala)	0.39	0.15	4.88	1, 27	<0.05
Rest of Amygdala (vs. LB Nucleus)	0.36	0.13	4.10	1, 27	<0.05
Amygdala (vs. Rest of Brain)	0.16	0.03	0.69	1, 27	0.41
Rest of Brain (vs. Amygdala)	0.14	0.02	0.55	1, 27	0.46

The effects of home range size on percentage fruit are the same as percentage fruit on home range size (see above).

Figure 5.17. Scatterplots displaying the relationships between **(a)** the residuals of the volume of the LB nucleus (removing the effects of the RoA) and percentage fruit in the diet, for strepsirhine and haplorhine primates and **(b)** the residuals of the volume of the RoA (removing the effects of the LB nucleus) and percentage fruit in the diet. The dots represent individual primate species and the line on each scatter-plot is a best-fit regression line.





Two final measures of ecology were analysed for each anatomical data set. First, activity timing (diurnal v nocturnal) was compared between species. The means and variances for activity timing are displayed in Table 5.14 and the overall results are summarised as histograms in Figure 5.18. The BL complex was found to be larger in diurnal species, $t(18) = 4.35, p < 0.001$, as was the LB nucleus, $t(31) = 5.89, p < 0.0001$. The other anatomical regions were larger in nocturnal species; amygdala, $t(16) = -0.44, p < 0.001$ and the CM complex, $t(18) = -0.42, p < 0.001$.

Table 5.14. Means and variances for anatomical measures (BL, CM, LB, and amygdala) varying by Activity Timing (Nocturnal v Diurnal).

	Nocturnal	Diurnal
Basolateral Complex		
Mean	68.16	73.02
Variance	9.97	10.24
Centromedial Complex		
Mean	31.70	26.98
Variance	10.47	10.21
Lateral Basal Nucleus		
Mean	6.02	8.63
Variance	1.02	3.12
Amygdala		
Mean	1.54	0.94
Variance	0.12	0.17

Stratification was also measured for each anatomical variable,. The means and variances are displayed in Table 5.15 and the overall results are summarised as histograms in Figure 5.19. The LB complex was larger in terrestrial species, $t(9) = -0.38$,

Figure 5.18. Histograms depicting the differences between the percentage size of the LB nucleus (as a percentage of the amygdala), the percentage size of the BL complex (as a percentage of the amygdala, the percentage size of the CM complex (as a percentage of the amygdala) and the percentage size of the amygdala (as a percentage of the brain) for 44 primate species (strepsirhines and haplorhines), where each species has been grouped dependent on activity timing (nocturnal or diurnal).

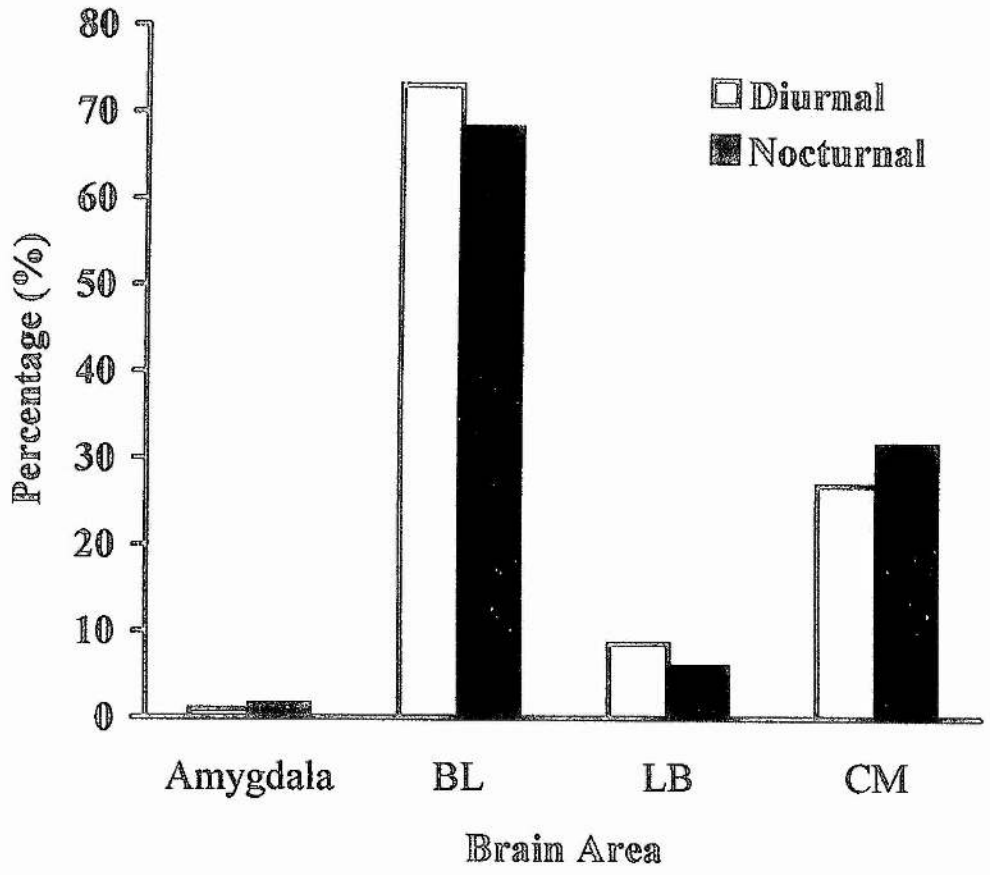
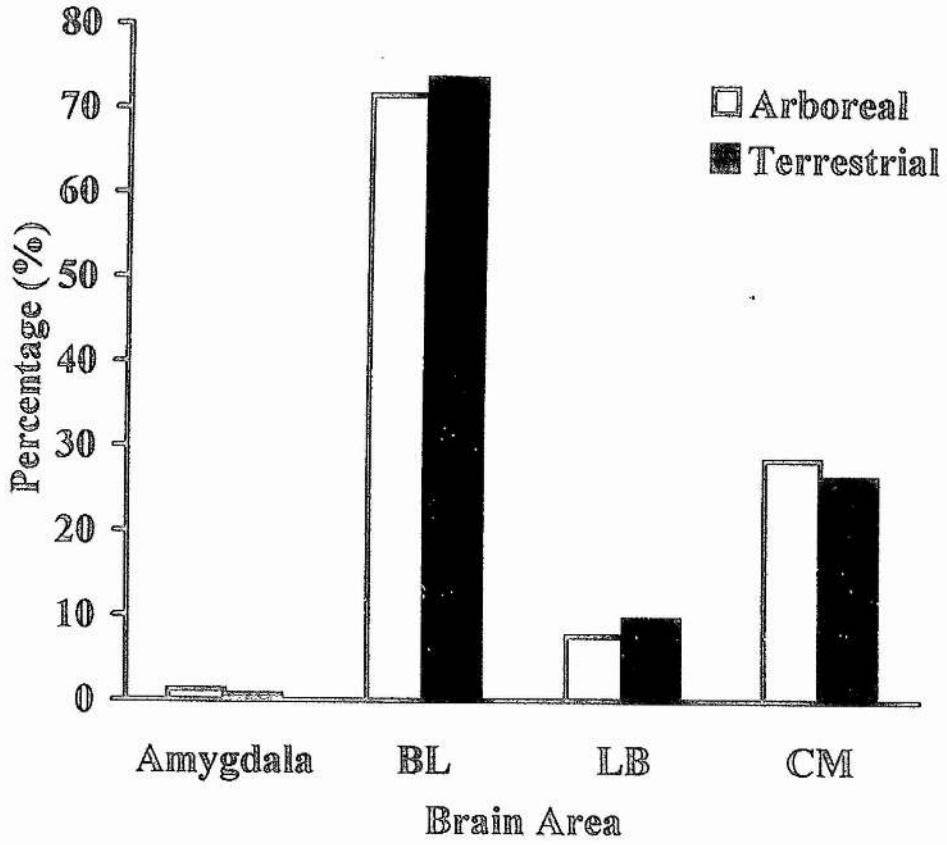


Figure 5.19. Histograms depicting the differences between the percentage size of the LB nucleus (as a percentage of the amygdala), the percentage size of the BL complex (as a percentage of the amygdala), the percentage size of the CM complex (as a percentage of the amygdala) and the percentage size of the amygdala (as a percentage of the brain) for 44 primate species (strepsirhines and haplorhines), where each species has been grouped dependent on stratification (arboreal or terrestrial).



$p < 0.01$. Arboreal species had a larger amygdala, $t(18) = 5.86$, $p < 0.0001$. There was no difference in stratification for the BL complex, $t(7) = -1.63$, $p = 0.15$ or the CM complex, $t(7) = 1.59$, $p = 0.59$.

Table 5.15. Means and variances for anatomical measures (BL, CM, LB, and amygdala) varying by Stratification (Arboreal v Terrestrial).

	Arboreal	Terrestrial
Basolateral Complex		
Mean	71.42	73.50
Variance	15.44	6.13
Centromedial Complex		
Mean	28.53	26.50
Variance	15.27	6.13
Lateral Basal Nucleus		
Mean	7.6	9.64
Variance	3.81	0.97
Amygdala		
Mean	1.19	0.58
Variance	0.22	0.02

5.3.3 CAIC analysis

CAIC analysis (Purvis and Rumbaut 1995) was used to determine the relationships between mean group size and residuals of volume of brain area (removing the effects of the corresponding brain region) for the LB nucleus, the BL complex and the CM complex. Residuals of the volume of the BL complex (vs. CM complex) were significantly correlated with mean group size, $r = 0.41$, $r^2 = 0.15$, $F(1,39) = 7.88$, $p < 0.01$. Residuals of the CM complex (vs. BL complex) were significantly correlated with mean group size, $r = 0.39$, $r^2 = 0.15$, $F(1,39) = 7.03$, $p < 0.01$. Finally, residuals of the

LB nucleus (vs. CM complex) were significantly correlated with mean group size, $r = 0.38$, $r^2 = 0.15$, $F(1,39) = 6.75$, $p < 0.01$.

5.4 Discussion

The results are summarised as follows. Group size appeared to be a relatively stable measure of social complexity. When grouping brain parts according to subjective measurements of group size (small, medium or large), a larger LB nucleus was related to medium and large groups (11+ individuals). A larger amygdala is found in small groups (1-10). The amygdala as a whole would, therefore not appear to be required for processing social information about large groups. This is may not strictly be true as the amygdala has increased in size allometrically with body weight. The amygdala has not increased as a percentage of the whole brain. This leaves the possibility that function has been transmitted to an area of the brain which is larger than would be expected for body weight, such as the neocortex. The BL complex was larger in large groups (+ 20 individuals), where as the corresponding CM complex was smaller in large groups.

Male group composition was also tested against brain part size. No relationships were found in the data. There was, however, an appreciable difference in the size of the LB nucleus according to male social structure, suggesting that the LB nucleus may be involved in general social behaviour *per se*, but not in processing behaviours specifically relevant to male sociality.

The relationships between brain area volume and mean group size were dependent on the measures used and partialling out the effects of a) body mass and b) a corresponding brain area, with which the area was heavily connected. When body mass was controlled (partialled out), all brain areas correlated with group size. When the effects of a corresponding brain area were removed all areas, except the amygdala correlated with group size. The most stringent correlations between group size and brain area were seen with the LB nucleus and the rest of the brain (RoB). Both areas correlated with group size when controlling for the effects of mass and either fruit or home range size. The rest of the brain includes the neocortex, which has been previously

shown to correlate well with mean group size (Dunbar 1992, Barton 1996). The LB nucleus is extensively connected with the neocortex (see Chapters III and IV), therefore it may have been predicted that the relationships between group size and the volume of the LB nucleus would be stable.

Similar relationships were seen with brain size and number of females in a group. All areas correlated with number of females (when body mass was controlled), but only the LB nucleus and the RoA when controlling for the reciprocal part. Again the LB nucleus and the RoB correlated with number females when controlling for mass and percentage fruit in the diet. When removing the effects of home range size, the LB nucleus, RoA, BL complex, CM complex and the amygdala correlated with number of females. The relationship with the LB nucleus again proved to be the most reliable.

Percentage time spent grooming was a good measure of social complexity, but the data available for this socio-cognitive variable were limited. Only the volume of the LB nucleus (partialling out the effects of body mass) correlated significantly with percentage grooming, as would be suggested by the LB nucleus' involvement in social behaviour (but mean group size did not correlate with % grooming). The LB nucleus and the RoA also correlated with percentage grooming when removing the effects of the corresponding brain area. This result is interesting as it is possible that grooming may require attaching emotional significance to incoming tactile information (from grooming), which may be processed in the amygdala. The likely candidate for processing in the amygdala would be the AB nucleus (part of the BL complex), which has many somatosensory connections. The LB nucleus also connects extensively to the somatosensory areas (see Chapters III, IV).

Volume of amygdala components also vary according to ecology. The LB nucleus (as a percentage of the amygdala) is smaller in insectivorous species and approximately the same size in folivores and frugivores, and the amygdala (as a percentage of the brain) is larger in insectivorous species and approximately the same size in frugivores and folivores. Insectivorous primate species are in the main prosimians, which are also nocturnal. The LB nucleus connects profusely with the visual system (ventral and dorsal processing streams), but not with the olfactory system (the olfactory

system is less well developed in simian primates according to the size of the nucleus of the olfactory tract, Stephan et al 1987, and the paleocortex or olfactory brain, Baron, Stephan and Frahm 1987). Catching insects may rely on lower levels of visual processing (such as processing motion, without form) than locating and eating fruit (although this seems unlikely).

Other ecological variables correlate with brain volume. The LB nucleus, BL complex, CM complex, amygdala and RoA all correlate with home range size (after removing the effects of body mass). When controlling for the corresponding brain area, the LB nucleus, RoA, amygdala and RoB all correlate with home range size. When controlling for mass and fruit, the BL complex and CM complex both correlate with home range size. The hippocampus correlates well with home range size, but the neocortex does not (Barton and Purvis 1994). The nuclei of the BL complex connect with the hippocampus (see earlier chapters), but what role the nuclei of the BL complex may play in remembering the location of foods (for example) is not known. The BL complex may be a part of a functional system coding emotional memory, e.g. location X = nutritious, tasty food = good feeling.

Percentage fruit in the diet also correlates with volume of brain area. After controlling for the effects of body mass; the LB nucleus, RoA, BL complex, CM complex and the amygdala all correlated with percentage fruit in the diet. Only the LB nucleus and the RoA correlated with percentage fruit in the diet, after controlling for the volume of the corresponding brain area. As suggested earlier, locating and processing fruit may require higher levels of visual processing, but choice may also be related to the hedonic appreciation of food (fruit A tastes nicer than fruit B, so more will be added to the diet if fruit levels can supply demand). Scott et al (1993) have suggested that the responses of amygdala neurons in the monkey, in particular the LB nucleus, are coding for the hedonic appreciation of food. This idea is congruent with the results of lesions of the monkey amygdala and temporal cortex (Kluver and Bucy 1939), where feeding behaviour becomes grossly disrupted. Recognition of objects as food was compromised, but the pleasurable aspects of feeding may also have been obliterated after lesions of the

temporal lobe. (Amygdala neurons also respond to the sight of certain foods; Ono et al 1983, 1989, Nishijo, Ono and Nishino 1988).

The LB nucleus and BL complex (as a percentage of the amygdala) are larger in diurnal species than nocturnal species, whereas the amygdala and CM complex are larger in nocturnal species. Information entering the LB nucleus (and BL complex) is predominately visual in origin, therefore, the LB nucleus and BL complex may be processing highly processed visual information (as appears to be the case, see earlier chapters). Auditory and tactile information also reaches these areas. Nocturnal primates predominately use olfactory means of social communication, which may be processed by the CM complex. The functional relationships described in this chapter would therefore be expected from known anatomical relationships.

The LB nucleus (as a percentage of the amygdala) is larger in terrestrial species, whereas the amygdala (as a percentage of the brain) is larger in arboreal species. Following the previous arguments, these relationships are to be expected from anatomy, as arboreal species have to rely on olfactory information where there is little light in the canopy, and terrestrial species can use visual methods of social communication due to increased light levels. Strangely, there is no evidence of size differences between stratification for the BL complex or the CM complex, which may be explained by other forms of modal information being processed by these areas, which is not contingent on visual processing. For example, the other nuclei of the BL complex may process auditory information which can be used as a form of communication in the canopy or on the ground. The main results are summarised in Table 5.16 (brain area removing effects of body mass) and Table 5.17 (brain area removing effects of corresponding brain area).

Table 5.16: Summary table of main results of relationships between brain area (removing the effects of body mass) and socio-ecological variables. √ indicates significant correlation, and X indicates no relationship.

Brain Area	Group Size	No. Females	% Grooming	Range Size	% Fruit
LB Nucleus	√	√	√	√	√
Rest of Amygdala	√	√	X	√	√
BL Complex	√	√	X	√	√
CM Complex	√	√	X	√	√
Amygdala	√	√	X	√	√
Rest of Brain	√	√	X	X	√

Table 5.17: Summary table of the main results of relationships between brain area (removing the effects of corresponding brain area) and socio-ecological variables. √ indicates significant correlation, and X indicates no relationship.

Brain Area	Group Size	No. Females	% Grooming	Range Size	% Frui
LB Nucleus (vs. RoA)	√	√	√	X	√
RoA (vs. LB Nucleus)	√	√	√	X	√
BL Complex (vs. CM Complex)	√	X	X	√	X
CM Complex (vs. BL Complex)	√	X	X	√	X
Amygdala (vs. RoB)	X	X	X	X	X
RoB (vs. Amygdala)	X	X	X	X	X

5.4.1 Amygdala and the evolution of social behaviour

Some of the predictions made in the introduction were found to be substantiated by the results presented above, whilst others were not. Neocortex ratio (volume of neocortex against the volume of the rest of the brain) has been used to predict the mean group size of primates (Dunbar 1992, 1995). The neocortex contains regions which when lesioned cause deficits in social behaviour and contain cells which may function in social recognition, interaction and action. It is important to note that lesions of and cellular responses in other regions of the primate brain also contribute to processing social stimuli. The amygdala is one of the regions (see Chapter II).

Anatomical connectivity, neuropsychological and neurophysiological studies in macaques, described in Chapter II, have revealed a divergence of function for the macaque amygdala's two component parts. This anatomical and functional separation of the macaque amygdala would seem to be present throughout the primate order (or at

least in simian primates). There appears to be a trade-off between the BL and CM complexes which is concerned with processing information about social group behaviour. This was predictable from the connectional analysis of Chapter V. It is therefore possible that the BL complex 'took-over' the role of the CM complex in social behaviour. This may be explained by the shift in method of social communication from prosimian to simian primates. Prosimians are nocturnal, arboreal and use vocal or primarily olfactory communication in social interactions. This is due to necessity (vision is difficult in the dark forest). Simians, by contrast, are not only vocal, but also highly visual (being diurnal and terrestrial, see Chapters II and III). The LTO nucleus (not analysed here, but minuscule or non-existent in simian primates) is connected with other olfactory structures and processes solely olfactory information. The CM complex has few cortical, but many subcortical connections, especially with the hypothalamus which may be involved in olfactory recognition and communication by sex pheromones (Karadi et al 1989), and the olfactory bulb (Carmichael et al 1994). The BL complex (and LB nucleus) by contrast have many cortical connections (see Chapters IV and V), particularly with 'higher' visual centres which contain neurons coding for the recognition of biologically and socially important stimuli, such as faces (Bruce et al 1981, Perrett et al 1982, Desimone et al 1984, Perrett and Emery 1994), whole bodies (Wachsmuth et al 1994), eye gaze (Perrett et al 1985b, 1992) and moving bodies (Oram and Perrett 1996). The BL complex itself contains similar types of neurons (Leonard et al 1985, Rolls 1984, Brothers et al 1990, Brothers and Ring 1993).

The shift in function from CM complex to BL complex, would also accompany a change from predominantly sexual behaviour in non-primate mammals and prosimians (controlled by the hypothalamus, see Lipp 1978, Lipp and Hunsperger 1978, Lloyd and Dixson 1988) to more complex forms of social cognition, highlighted by the Machiavellian Intelligence hypothesis (see papers in Byrne and Whiten 1988, Whiten and Byrne 1997) in simians. This hypothesis would also fit with the anatomical data.

5.4.3 Conclusions

Previous studies of the connection between brain size and socio-ecological variables have ignored the role which the amygdala and the amygdala's component parts may have played in the evolution of primate social behaviour. The results of this chapter have highlighted significant relationships between the volume of the BL complex, and in particular, the LB nucleus and various predictors of complex social functioning. The possible prominence of the LB nucleus in primate social evolution was suggested by the connectional data discussed in Chapter IV. The LB nucleus appears to perform the same or similar social functions in a large number of primates, not just macaques. Neuropsychological tests of social information processing in human patients with amygdala lesions suggest that the amygdala also functions in aspects of human social behaviour (Adolphs et al 1994, 1995, Young et al 1995, Breiter et al 1996, Calder et al 1996, Young et al 1996, Scott et al 1997,)

The volume of the LB nucleus and the other nuclei of the BL complex are also related to aspects of ecological processing, which may be related to emotional and social behaviour. There is no previous evidence that the amygdala is involved in processing information about the location and extraction of foods or in specialising in eating different types of food, although amygdala neurons do respond to the sight of certain food, such as water melons (Ono et al 1983, 1989). Two possible functions may be social learning of complex food processing skills (Byrne and Byrne 1993, Russon, 1997, see also Chapter VII) or as suggested earlier attaching hedonic value to different food types (Scott et al 1993).

Chapter VI

General Neurophysiological Methods

6.0 Subjects

Subjects were two juvenile rhesus macaque monkeys, one male (S; weight, 5-7 kg) and one female (E; weight, 8.0 kg). The subjects were born and reared in an established, registered UK breeding colony. Throughout recording and training periods (over two and a half years), the monkeys were housed separately from the colony, but still remaining in visual and auditory social contact with the other monkeys. One monkey (S) was used in the gaze following study (Chapter IX) and had been previously used in another behavioural test, involving the use of human eye gaze to determine the presence of a peanut reward (Pettigrew, Forsyth and Perrett 1993, unpublished observations).

6.1 Pre-surgical training

Before light-discrimination training, the subjects were trained to enter a primate chair voluntarily, and sit comfortably for up to 4 hours. The subject was trained to enter a travelling cage, which was moved into the laboratory. Further training, enabled the subjects to safely and spontaneously enter the primate chair and place his/her head through the neck plates for further head restraint (under Home Office Licence).

The subject's food and water was restricted once training had begun. Food in the subject's home cage was restricted to dry pellets (with fruit and vegetables at weekends) and fruit and nuts were given during training and recording sessions. Water was withdrawn for up to 24 hours (usually overnight) between training and recording sessions and was available during training and *ad lib* after training. This regime allowed the

subjects to control their own water intake and also maintained the subjects' performance on the light-discrimination tasks.

The first stage of training required the monkey to lick juice from a pair of licktubes, which were attached to the primate chair in front of the monkey. The licktubes were connected first to a solenoid driven pump system (subject E). The liquid-reward system was later converted to a two-syringe, two-valve pipette (Microlab 941; Hamilton, Dundee, UK). The tubes dispensed liquid when the circuit between the tubes and the primate chair was closed (by the subject licking). Reward, such as sweet blackcurrent juice (Ribena) or sugared water was dispensed as an incentive to lick during training.

The subjects were trained on an LED colour discrimination task. LED displays were imbedded in the white projection screen facing the monkey (4 m from the primate chair). Five LEDs were positioned in the screen (centre; +/- 10^{0} above and below the central LED or +/- 15^{0} to the left or right of the central LED). The monkey was trained to discriminate the colour changes of the LED in the centre of the screen (red or green) and an LED attached to the primate chair close to the subject. The LED first changed colour at the discretion of the experimenter. Later in training, the presentation was controlled by the computer in a pseudo-random order. When a juice reward was dispensed, the LED changed to green (after a 0.5 sec tone). When a mildly aversive, weak saline solution was dispensed, the LED changed to red (also after a 0.5 sec tone). The monkey learned to lick when a green light was displayed and withheld licking when a red light was displayed. This task required that the subject maintained fixation on the central LED (for approximately 1 sec).

6.2 Implant construction

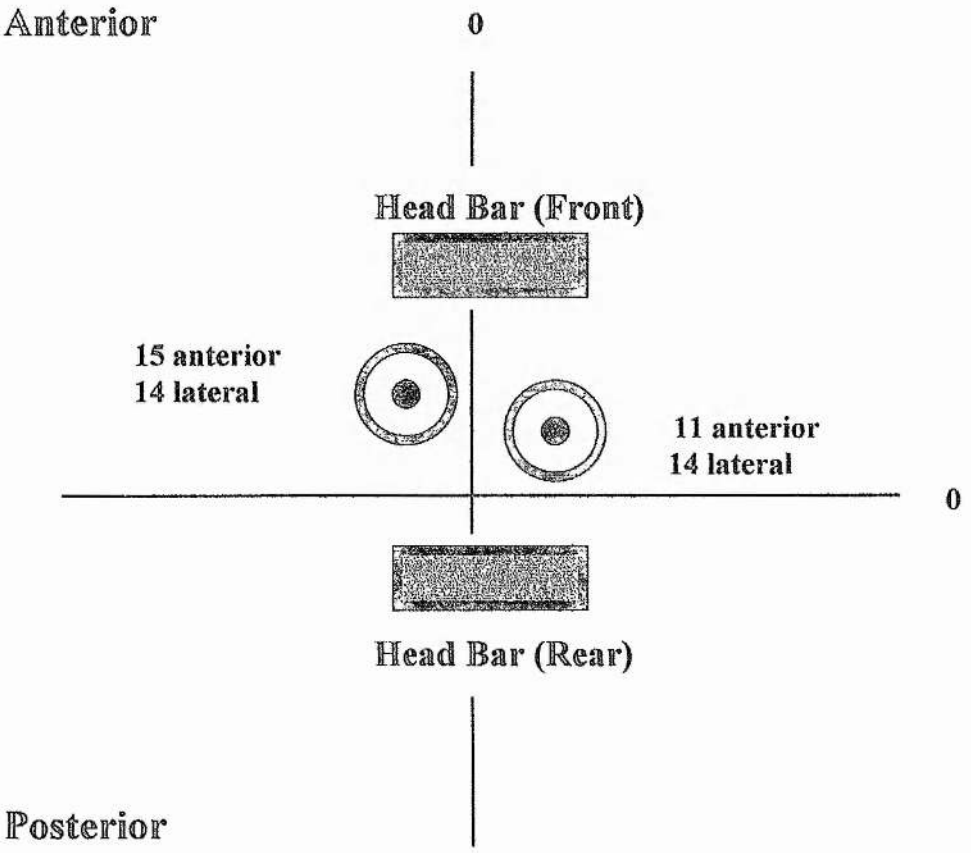
Once the monkey was successful on the visual discrimination task, the monkey was prepared for surgical implantation of the stainless steel recording wells. First, the stereotaxic implant was made. This consisted of two stainless steel David Kopf wells and two restraining head bar holders, made from PTFE or Tuffnal. The stereotaxic co-ordinates for each well were determined for each monkey from previous subject co-

ordinates. The co-ordinates which enabled ease of entry to the STS were 15 anterior/14 lateral in the left hemisphere and 11 anterior/14 lateral in the right hemisphere (see Figure 6.1). A scale diagram of the implant (1:1) was made using graph paper, showing the positions of the wells and the position of the head bars relative to the wells. A sheet of glass was then placed over the diagram and the various components of the implant placed in the appropriate positions on the glass on the graph paper diagram (using Blutack). Dental acrylate (Autenal Dental Products Ltd., Harrow, UK) was then poured sparingly onto the parts of the implant, loosely joining them together. Excess dental acrylic was removed using a dental drill. The implant was removed from the glass by "floating-off" with water.

6.3 Surgery

Twenty-four hours prior to surgery, the monkey's access to food was restricted (including forage). Twelve hours before surgery, the monkey was water restricted. In preparation for surgery, the monkey entered a travelling cage and was given an injection of ketamine (0.5 to 1.0 ml depending on weight of monkey; 10 mg/kg Vetalar, Park Davis & Co., Gwent, UK). This sedated the monkey, so that the legs (for anaesthetic injection) and head could be shaved. Liquid paraffin oil was placed into the monkey's eyes for protection and to stop the eyes from drying up. The shaved head was swabbed with alcohol and tincture of Iodine. To reduce secretions, particularly saliva, during the operation, Atropine (1 ml of 600 μg/ml) was injected. A wide acting anti-biotic was also injected (1 ml duplocillin; Propen) to prevent infection. Before being taken into theatre, an intravenous cannula (as part of a Butterfly vein set, JERUM, Surflo IV catheter) was inserted into a large vein in the leg, which allowed the administration of a barbiturate anaesthetic (Sagatal; 60 mg/ml; May & Barker Ltd., Dagenham, UK). This cannula was connected to an infusion set (Bioset) and Hartmann's solution drip (Baxter) in theatre via a three-way valve. This provided a continuous flow of saline to enter the vein and the option to administer Sagatal.

Figure 6.1. Diagram of the implant co-ordinates for subjects Esther and Steve. Top of the diagram is anterior and the bottom is posterior. The implant consists of two Teflon, ceramic or plastic tubes through which the restraining head bars can be fitted and two stainless steel wells which the David Kopf micro-positioner is attached.



Full sterile procedures were observed in theatre. The surgeons were clothed in sterile gowns, hats, masks and gloves and equipment was prepared by autoclaving or bathing in alcohol or Cetavalon. Other assistants and observers were clothed in gowns, hats, masks and gloves and remained clear of the sterile area. The monkey's head was placed into the stereotaxic frame, held in position by the ear-bars into the external auditory meatus, teeth-bars and orbital ridge grips. The monkey was positioned onto a diathermy base plate and wrapped in a fleece blanket and diathermy cover. Body temperature was kept at approximately 37 ^{0} C, thermostatically controlled with a rectal thermometer probe. To maintain a watch on breathing rate (30-40 breaths per min), the monkey was also covered by an inflatable breathing monitor blanket linked to a counter.

One incision was made from just above the eyebrow ridges to the back of the crown of the skull. The skin was then reflected and held in position with the use of haemostats. Connective tissue was scrapped away using bone scrappers and localised bleeding was quaterised using a diathermy needle. Before drilling, the implant was lowered onto the skull surface and the position of the two recording wells was drawn onto the skull using a china-graph pencil. The areas marked were then drilled out, using a dentist's drill, being careful not to damage the dura, underneath the skull. This procedure was performed under constant saline irrigation to stop the temperature of the skull rising above 50 ^{0} C, which would cause bone necrosis. Once the two well holes were cut and removed, the implant was lowered on the skull to verify the position of the required stainless steel T-pieces (1 cm length, 0.3 cm width), screws (1 cm length) and the holes. 6-8 small holes (1 cm length) were then drilled into the skull and the T-pieces and screws were placed into position. The implant was then re-lowered and dental acrylic placed around the implant to secure it in place. Dental acrylic was built up around the wells to make an effective seal and around the head bars so that they could withstand pressure once the animal was restrained in the primate chair.

Throughout the operation the sedation of the animal was checked using various pain reflexes (foot pressure twitch reflex) and if deemed necessary, further doses of anaesthetic were administered. A cumulative dose of 3 ml (Esther) and 5 ml (Steve)

Sagatal (initial dose X ml, with additions of between 0.25 and 0.5 ml, every 20 minutes at the start of the operation, with longer gaps between administration later in the operation).

The monkey was then returned to the home cage and wrapped in a fleece blanket. The monkey was given a minimum of 4-7 days to properly recover fully. The monkey was then retrained on the visual discrimination task until satisfactory performance was achieved. The dura in the wells was kept clean every 1-2 days after the operation with saline swabs and an anti-bacterial agent (PEP, 3% powder).

6.4 Electrophysiological Recording Methods

For each recording session the wells were cleaned using diluted antiseptic disinfectant. Before inserting the metal guide-tube (length 60 mm) and the electrode, 0.1ml of topical local anaesthetic (lignocaine hydrochloride, Xylocaine, 40mg/ml; ASTRA Pharmaceuticals Ltd.) was applied to the surface of the dura. A David Kopf micro-positioner was then attached to the appropriate recording well and a transdural guide-tube (internal diameter 0.6 mm) was inserted 3-5 mm into the brain at the correct co-ordinates determined before recording. The co-ordinates were chosen from previous experimental animals, previous tracks and on the number of penetrations made into a particular position. A tungsten in glass microelectrode of measured length and tip size (outer diameter 0.5 mm, Merrill and Ainsworth 1972), was inserted through the guide-tube and advanced into the target recording area using a hydraulic micro-drive (David Kopf 607W). The depth of every cell tested was noted from the micro-drive. The target area was the STPa in the anterior part of the upper bank of the superior temporal sulcus (areas TPO and PGa of Seltzer and Pandya 1978; see Chapter III).

The electrical signals were amplified using a Neurolog (NL104) amplifier, filtered with a 50 Hz notch filter together with low pass (300 Hz) and high pass (20 Hz) filters (Neurolog NL125) and displayed on a fast time base oscilloscope and audiomonitor. These signals were then converted to TTL pulses by a spike processor (Modified Digitimer DM130; threshold voltage window for discriminating individual action potentials). The TTL pulses were used to form peri-stimulus time histograms (PSTHs)

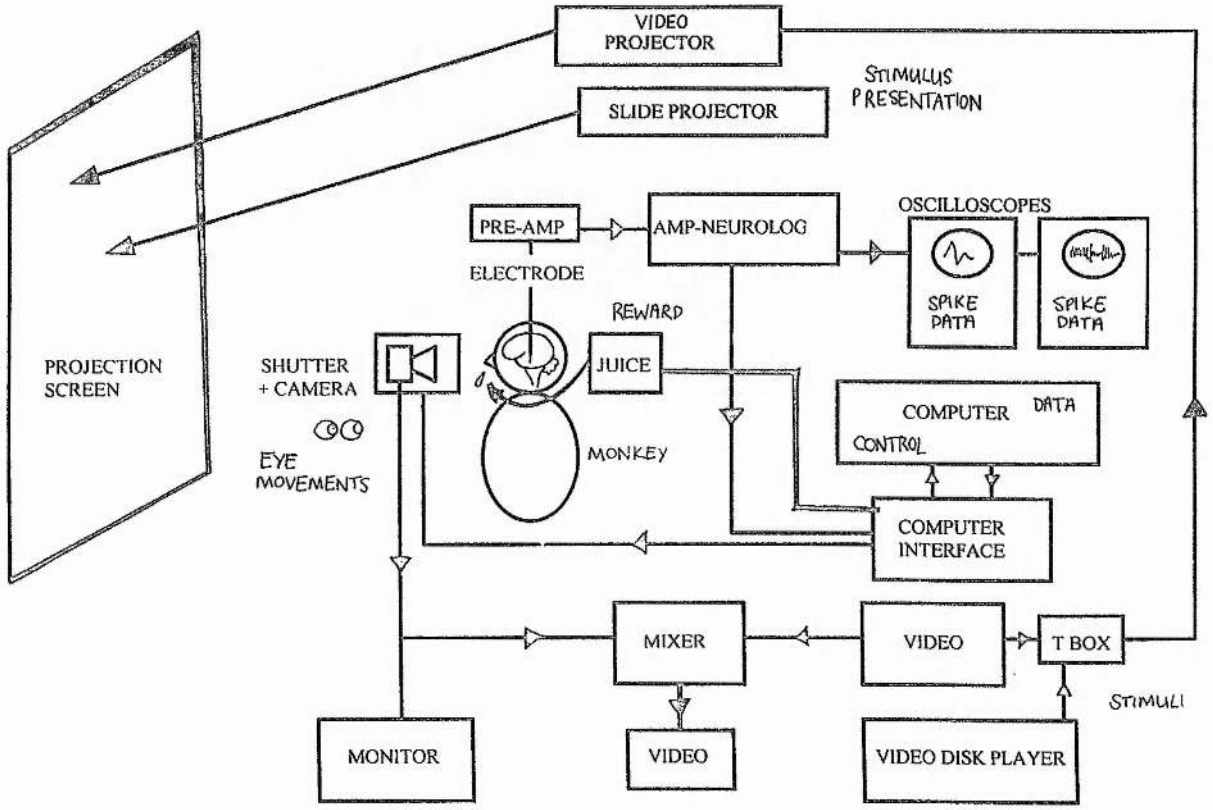
which were displayed as 250 bins of approximately 5 ms duration. During data collection, there was a pre-stimulus sample period of either 200-300 ms and a post stimulus time period of 1 second (these were set by the experimenters). Data was collected on an AT compatible PC microcomputer (Dell 386), and CED 1401 (Cambridge Electronic Design) using custom software (Dick program, Oram 1996). A schematic representation of the physiological laboratory, including data collection methods and visual presentation methods is displayed in Figure 6.2.

6.5 Data analysis

Before testing for specificity, cell responses were tested clinically, without quantitative testing methods. These tests were used to determine the modality of the cell being tested and whether cell responded to motion or static images. Once a particular cell type was determined, the cell was tested more formally with the appropriate test stimuli. Cell responses were measured from the true stimulus onset time, or the time when a 20 cm^2 transparent computer controlled shutter (Screen Print Technology Ltd.) was opened.

Eye movements were monitored using an in-built infra-red camera [Compact medium-high resolution camera (JVC), RS Components; resolution: 500 horizontal by 582 vertical pixel, and a wide angled lens (16 mm), light sensitivity 0.5 lux (at F 1.4)]. Cell responses were recorded 100 ms after stimulus presentation, for 250 ms (a time period of 500 ms was sometimes recorded). Visual stimuli were tested with 5 trials in a computer-controlled pseudo-random order, with the data collected and on-line analysis performed by the microcomputer. On-line analysis enabled the experimenters to determine what properties the cell had, so that further appropriate tests could be performed. Cell depths were recorded from the David Kopf micropositoner, but were also recorded by taking X-radiographs after each recording session.

Figure 6.2. Schematic representation of the physiology laboratory set-up. The subject sits in the primate chair facing a white projection screen onto which visual stimuli are presented. Cell responses are detected by the electrode, which are amplified and filtered by the Neurolog system, the data is then collected by the computer, which also controls the pseudo-random order presentation of the visual stimuli, via the video-disk player, video cassette recorder. Slide and 3D stimuli are also presented in pseudo-random order.



6.6 Histology

6.6.1 Perfusion

After a sufficient number of recording sessions had been completed, the animal was killed and perfused for anatomical and histological studies. Thirty minutes before perfusion, the monkey was given an anti-coagulant (Heparin 5000 units/1.5 kg body weight). The monkey then received an injection of Ketamine (1.0 ml Vetalar) and finally a lethal intravenous injection of Sagatal. This placed the animal into a deep coma, which was verified by the absence of a gabella reflex (eye-lid closure after the cornea is gently touched).

The monkey was perfused transcardially (via the heart). First, the thorax was opened to expose the heart and a large bore cannula (internal diameter 2mm) was inserted into the left ventricle. A puncture was also placed into the right atrium so that blood and the pre-fixative solution would flow from this exit point. 5 litres of pre-warmed (37 ^{0} C) pre-fixative (0.1 M phosphate buffered saline + 0.2% $NaNO_3$) was passed through the heart by the use of a centrifugal pump (C16-C, Charles Ansten Pumps Ltd.) positioned approximately 1 m above the body. After the pre-fixative had passed through the articulatory system, the fixative solution (phosphate buffered 4% paraformaldehyde and 0.5% glutaldehyde) was passed through a perfusing cannula into the left ventricle and into the ascending branch of the aorta. The descending aorta was clamped shut.

6.6.2 Sectioning, mounting and staining of sections

Once the brain was thoroughly fixed, the brain was removed from the skull using bone cutters. The brain was blocked (i.e. cut at a vertical angle, 90^{0} from the horizontal) at anterior 25. The cerebellum, posterior to the corpus callosum (approximately posterior 10), was left on the brain and used to form a base for sectioning. The brain was also marked on one side (with a scalpel) to discriminate left from right when mounting

sections. The brain was then sunk in successively higher concentrations of sucrose (10, 20 and 30 %) and left in the refrigerator at 4 ^{0} C.

One litre of isopentane was placed into a metal container and cooled to approximately minus 45 ^{0} C. The liquid was cooled by adding dry ice. The stage (chuck) of the cryostat (Bright Instruments Co., Huntington, UK) was then placed into the cryostat to check whether the blade would pass over the whole of the stage and entire brain. Before the chuck was attached to the cryostat, a smaller loose block was attached to the chuck at the bottom and back of the chuck. The chuck was then removed from the cryostat. Embedding compound (OCT) was trickled down the brain from top to bottom, so that it entered all the sulci. The posterior end of the brain was then placed onto the chuck platform. The chuck was placed into a holder and lowered into the freezing isopentane. The temperature of the isopentane was kept below minus 36 ^{0} C by adding more dry ice. After 20 minutes, the brain was removed from the isopentane and put into the cryostat, upside down (i.e. the ventral surface was dorsal).

The brain was left to equilibrate for 1 hour at minus 24 C in the cryostat. Brain sections of 25μm thickness were taken every 1/4 mm and collected in bays filled with 0.1M phosphate buffer and 0.9% NaCl (half-filled). A photograph of the brain block was taken every 1 mm using a still camera (Nikon) at a fixed position, on a fixed tripod. A label with the section number and animal name was fixed underneath the brain block after each photograph.

Sections were removed from the blade with a small paint brush on either side of the section and lifting the section away from the blade and placing into the appropriate collection bay (marked with section number). Sections were free-floated in phosphate buffer and were transferred to dishes containing tap water, for mounting with a small brush. The pre-coated microscope slides were marked with the appropriate section number (using a glass pencil) and lowered into the water. The sections were guided onto the slides making sure that the sections were the correct orientation. When the sections were reasonably flat on the slide, the slide was dragged up from the water while gently pulling the section straight. The sections were then left to dry in the air and placed onto slide trays.

The sections were stained for Nissl substance (cell bodies) using cresyl violet stain. First, the sections were placed in Xylene for 2 minutes, transferred to absolute alcohol for 3 minutes and then 50% alcohol for a 3-4 rinses. After rinsing in tap water, the sections were placed into cresyl violet stain for 1 $^{3/4}$ - 2 minutes. The sections were left in water for 2-3 minutes or until the excess stain had been rinsed off. Again, the sections were rinsed in 50% alcohol, then unadulterated absolute alcohol, absolute alcohol and finally Xylene (length of time depending on the time left in the alcohol; long alcohol = short Xylene). The sections were then cover-slipped and excess xylene and bubbles removed. The sections were stored in section boxes until microscopic investigation.

6.7 Reconstruction of electrode tracks

Before the brain was sectioned, anatomical stereotaxic marker probes (cannula) were placed into the brain at various stereotaxic positions, for example in the STS and the centre of the amygdala. The position of the probes was determined from the previous electrode tracks and stereotaxic co-ordinates using the David Kopf micro-positioner. Indian ink (Windsor & Newton) was injected (5µl at 5-10mm intervals) using a glass micro-syringe (Scientific Glass Engineering PTY, Ltd.) attached to plastic tubing and cannula containing dye.

Vertical probes were inserted stereotaxically at positions -10mm, 0mm, 10mm and 20mm anterior, 15mm lateral; into the brain to reconstruct Anterior/Posterior (AP) position of tracks. Horizontal probes were inserted bilaterally at -10mm, 0mm, 10mm and 20mm depth relative to the auditory meatus. The probes were inserted, so that when slides and tracings of brain sections were viewed, they could be aligned properly so that electrode tracks could be reconstructed relative to one another. These probes were also recorded with X-radiographs.

After each recording session, frontal and lateral X-radiographs were taken of the monkeys head using a Portable X-ray machine (Type MX-2). The microdrive was detached from the David Kopf, with the electrode remaining in the brain. X-rays were

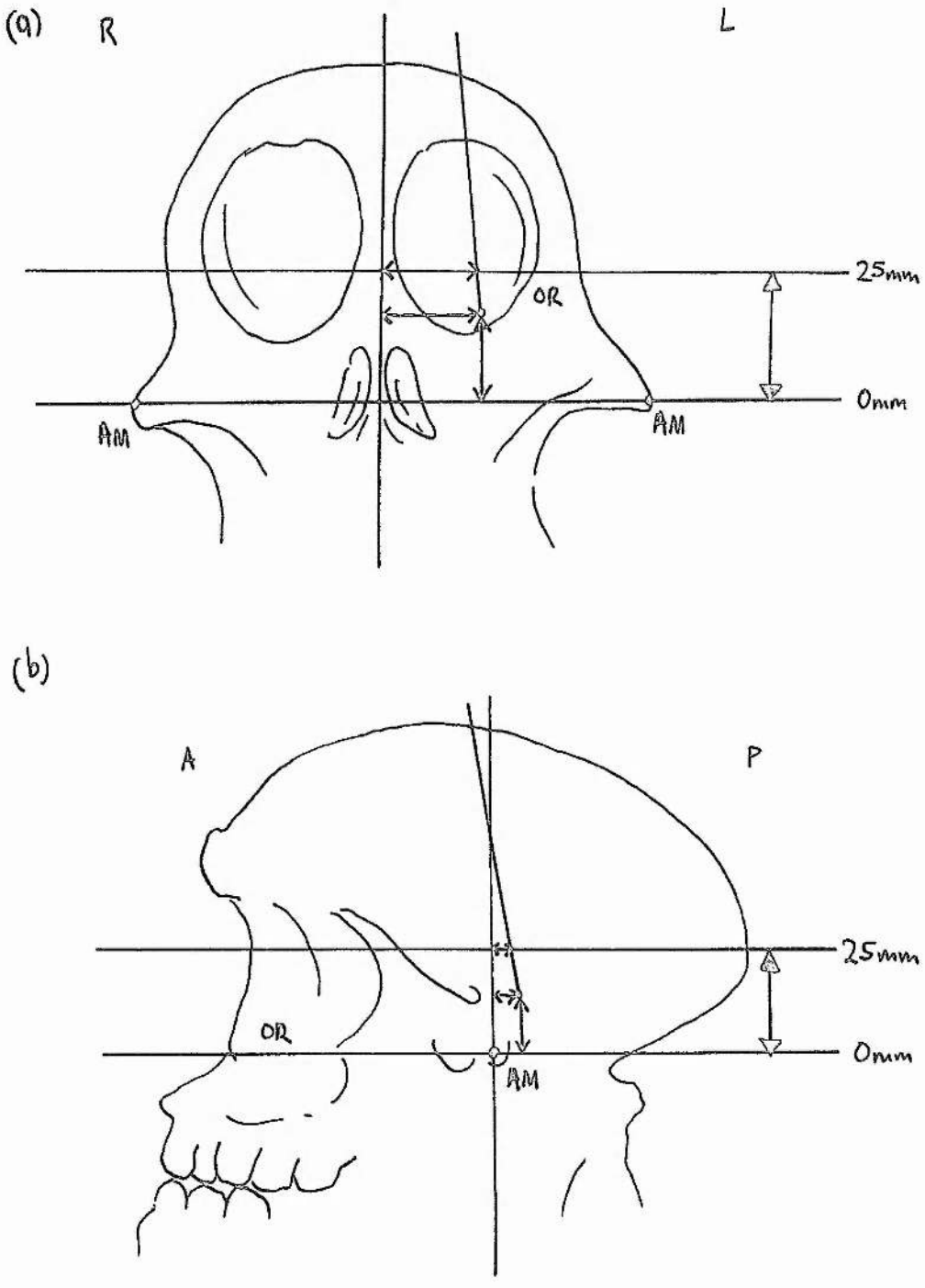
taken with exposure times of 5-6 seconds at 16 kV. X-rays were taken at the same distance from the skull for each session (10cm) and were taken whether cells were found or not. An initial clear set of x-ray photographs were used as templates for subsequent x-ray measurements.

The depth, A/P position and laterality of the electrode tip were measured in frontal and lateral X-radiographs. The depth was defined relative to a horizontal line through the auditory meatus (zero plane, height 0mm) and a horizontal line drawn 25mm above the zero plane. The A/P position was defined relative to a perpendicular line through the auditory meatus and horizontal line drawn through the auditory meatus and under the orbital ridge. Laterality was defined relative to the perpendicular mid-line, equidistant between the eye sockets (see Figure 6.3).

From the X-radiograph co-ordinates, the 3-D trajectory of the stereotaxic probes could be determined. The electrode coordinates taken from the X-radiographs were matched to tracings of the photographic slides taken after every brain section. The slides were projected onto a white wall covered with clean white tracing paper. Each section was aligned so that the cryostat chuck was in a constant position. For each projected slide, the position of the various Indian ink probes were recorded with anatomical landmarks, such as the external boundary of the cortex and the grey-white matter boundary within the gyri and sulci.

The tracings were then stored onto a personal computer using specially developed software (Oram 1996) by tracing the sections into a computer programme (using a mouse). The brain maps were then used in the reconstruction of electrode track and cell positions, which had been stereotaxically verified.

Figure 6.3. Reconstruction of electrode track position from X-ray photographs. **(a)** Drawing of frontal X-radiograph displaying macaque skull with auditory meatus (AM) and orbital ridges (OR). The horizontal (0mm) line passing through the AM and under the ORs is a reference for the depth measurements for the tip of the elctrode. A line is drawn 25 mm above the zero line so that two coordinates for the depth can be entered into the computer. The perpendicular line positioned equally between the two eye sockets and the nasal cavities is a reference for the laterality measurements. **(b)** Drawing of lateral X-radiograph displaying macaque skull with AM and OR. The horizontal line passing through the AM and under the OR is a reference for the depth measurements for the tip of the electrode. Again a line is drawn 25mm above the zero line. The line perpendicular to the zero plane also passes through the AM and is a reference for the A/P measurements.



Chapter VII

Neurophysiology of Perceiving Purposive Behaviour

Attention & Intention

"Only species that also possess the ability for highly differentiated movements of the appendages and individual body parts, and a reliable use of such movements in their own anticipatory dealing with objects not within their grasp, will provide group members with any reliable potential cues."

Menzel (1974b, p. 132)

"Walking is certainly purposive....It is also informative; for example, the rate of speed with which someone is walking suggests to us how interested he is in his goal."

Chomsky (1967, p. 73)

"Purposive movement is defined...as motion that cannot adequately be described without referring to some object external to the animal."

Menzel (1974b, p. 133)

7.0 Summary

The ability to discriminate where others are attending (Chapter IX), where they are moving to and what they are interacting with, is of primary importance for understanding others' behaviour (Brothers 1990, 1994). Visual representations of another's attention, motion and action are derived in various regions of the brain (Perrett and Emery 1994). These neural systems specialising in the analysis of others' social behaviour may be precursors used in the sensory analysis of the contents of the minds of conspecifics (Brothers 1992, Brothers and Ring 1993). It is the purpose of this chapter to 1) review studies of primate purposive behaviour, in particular social learning, imitation and social attention and 2) to discuss the behavioural abilities of primates as providing a

functional context for interpreting the results of the neurophysiological study described within this chapter.

7.1 Introduction

7.1.1 Perceiving Purposive Behaviour & Theory of Mind

Before discussing some of the possible evidence pertaining to reading purposive or intentional behaviour in others, it is important to clarify what is meant by these mentalistic terms. The concept of a "theory of mind" or "mindreading" or "metarepresentation" or "intentionality" (Baron-Cohen 1994, Whiten 1994, 1997) has been discussed recently by a number of authors who are either against the idea that animals and in particular non-human primates have a concept of other's minds (Heyes 1997) or for the idea that, at least some primates (namely the great apes and humans) have such concepts (Povinelli 1996, Whiten 1996, 1997). It is not the purpose of this chapter or this thesis to discuss the pros and cons of such arguments (these have be made on multiple occasions elsewhere, see previous references). This chapter will, however, discuss the evidence for purposive "behaviour reading" in monkeys, apes and to a lesser extent humans, how these abilities may be dependent on interpreting basic visual signals and how these signals may be coded in the brain.

Theory of mind was a term coined by Premack and Woodruff (1978), attempting to describe the complex behavioural reactions of a language-trained chimpanzee called Sarah, in response to a video sequence. In the task, Sarah watched video films of a human actor attempting to solve a problem, such as reaching for an out-of-reach banana. Sarah was then presented with a collection of photographs, one containing the solution to the problem, such as a stick to reach the bananas. Sarah consistently chose the photograph with the solution, suggesting to Premack and Woodruff that she knew that a problem had to be solved, that the actor was the one attempting to solve the problem and that only one course of action could solve the problem. This suggested to them that

Sarah could infer intentions, desires and beliefs from basic perceptual signals provided by the actor.

Many attempts have been made to determine whether monkeys, apes and humans can attribute mental states to others. Those efforts will be detailed in the three sections below which focus on social attention, intention and imitation. The most convincing evidence for possession of a theory of mind has been shown for human infants (however, adults have not been tested implicitly). It has also been suggested that children with the developmental disorder of autism have deficits in theory of mind (Baron-Cohen, Leslie and Frith 1985).

(a) Mental significance of attention

The behavioural evidence for monkeys' and apes' awareness of other's attention cues and the ability to use attention cues to locate objects in the environment or to determine their emotional state of mind is discussed in the gaze following and joint attention study of Chapter IX.

The purpose of this section is to evaluate the role that analysing another's gaze (eye position, head view or pointing) may play in determining what the intentions of others are. Non-human primates may not infer intentions from the presence or direction of the eyes. The eyes may only be used to communicate another's emotional state (such as anger displayed as a threat), or to communicate the presence of objects within the immediate environment (see Chapter IX).

There are many instances in the primate literature which suggest that some primates may use their own gaze to convey information not just of an emotional or referential nature. Gaze following may be utilised by primates when soliciting for help from conspecifics when challenged by or challenging other group members. Soliciting help or an invitation to co-operate against a third party has been described for baboons (Kummer 1967, Packer 1977, Walters and Seyfarth 1987) and vervets (Cheney and Seyfarth 1990b). Vervet monkeys use quick, furtive glances between an aggressor and a potential helper, to gain support from the potential helper. The aggressive monkey needs to be attended to, both by the monkey soliciting help, and the potential helper. The

intentions of the soliciting monkey may then be determined by the helper. The object of attention needs to be known to a high degree of accuracy in possibly volatile situations. Soliciting has been described for *Papio anubis* (olive baboons) as:

"a triadic interaction in which one individual, the enlisting animal, repeatedly and rapidly turns his head from a second individual, the solicited animal, towards a third individual (opponent), while continuously threatening the third"

(Packer, 1977, p. 441)

Knowledge that other monkeys and apes automatically follow gaze may be utilised by some clever individuals in the species, during complex behavioural situations. In a database of primate tactical deception, Whiten and Byrne (1988a) describe an anecdote where they observed a young baboon apparently using gaze direction cues in a possibly deceptive communicative role. Baboons and vervets usually stare and make calls at predators in the distance (Whiten and Byrne 1988a, Cheney and Seyfarth 1990b). In the following anecdote, the subadult ME appeared to use this information to his advantage.

"subadult male ME attacks one of the young juveniles who screams. Adult male HL and several other adults run over the hill into view, giving aggressive pantgrunt calls; ME seeing them coming, stands on hindlegs and stares into the distance across the valley. HL and the other newcomers stop and look in this direction; they do not threaten or attack ME"

(Whiten and Byrne 1988a, p. 237)

Whiten and Byrne suggested that subadult male ME learnt that his own attention was a salient cue which could be used to deter others from chasing him. In this example, a predator (or other interesting object) was not within the field of view (or the object of ME's attention). Attention appeared to be an automatically interesting cue which was distinguishable enough to disrupt the actions of the pursuing animals. Whiten and Byrne (1988a, b) discuss many instances where an individual manipulates another's use of attention cues, as a form of deception.

How non-human primates use gaze in intentional communication, and understand the meaning behind this volitional use has only started to be tested experimentally. One recent study has highlighted one aspect of this use. Gorillas can successfully use their gaze to refer to objects and to direct humans' attention to objects and the gorilla's behaviour (Gomez 1990, Gomez 1991). Gomez tested an infant gorilla with a problem (similar to Kohler's problem-solving experiment (1925) with chimpanzees). Gomez found that the gorilla not only used conventional objects to solve the problem, but also used the experimenters as *social objects*.

An infant gorilla was placed into a locked room with a latch to lock the door (out of reach of the gorilla), a box high enough to reach the latch and a human experimenter. The infant gorilla used four different strategies to attempt to reach the latch. First, the gorilla dragged the box under the latch and climbed onto the box. Second, the subject dragged the experimenter under the latch, to climb on the experimenter and reach the latch. Third, the gorilla gently lead the human experimenter to the door while looking between the experimenter's eyes and the latch (the goal, or object of attention). Finally, the gorilla would look between the experimenter's eyes and the latch without leading the experimenter (Gomez 1990). By looking at the eyes and face of the experimenter, the gorilla could be said to be directing the attention of the experimenter to the focus of the gorilla's own attention, namely the latch. This may be similar to the baboons described earlier who solicited help by looking continuously between the goal of their attention (an opponent) and a solicited helper (Packer 1977). The gorilla may have been checking to see that the experimenter was still attending to the latch and to the gorilla's actions. The gorilla also seemed to use eye contact to monitor if the human was attending to the gorilla's request that the experimenter acted (Gomez 1990).

Distinguishing another's visual perspective from one's own is thought to be an important step to interpreting their intentions and thoughts about the world. Kummer et al. (1996) attempted to train long-tailed macaques (*Macaca fascicularis*) to take a juice reward, only if a human experimenter was not in a position to observe them taking the reward. The experimenters threatened the monkeys if the monkeys took the reward whilst in the experimenter's view, however, the subjects behaved equivalently, drinking

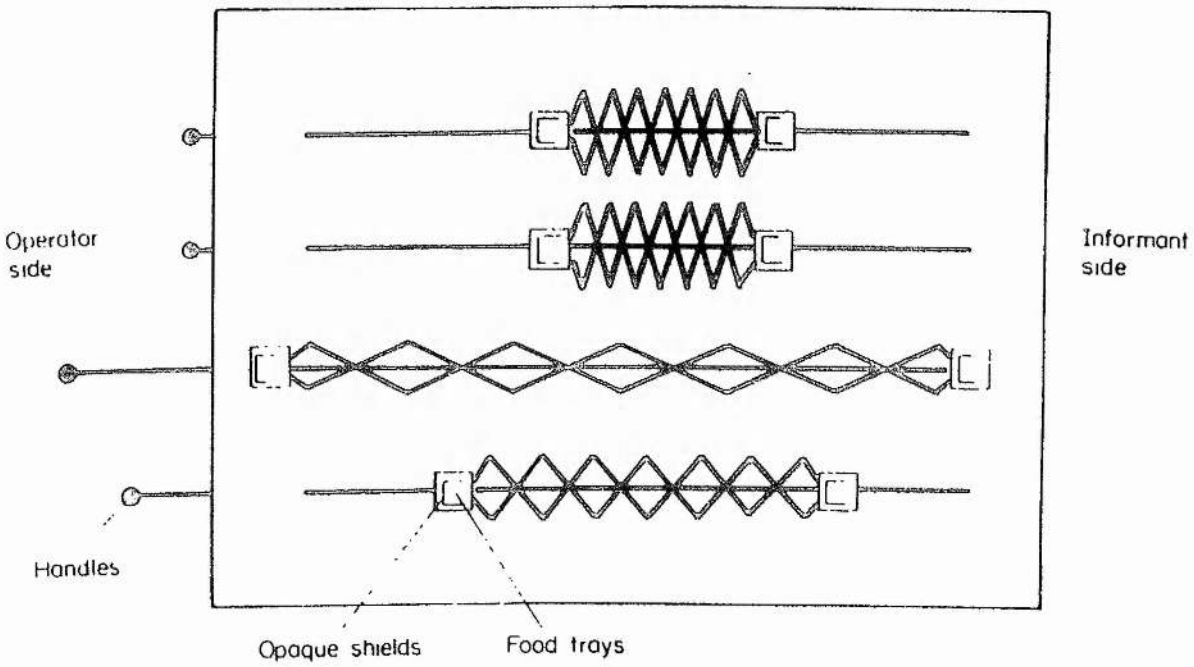
juice reward out of view of the experimenter (hidden behind an occluder), or in front of the experimenter. Kummer et al. interpreted this as a lack of perspective-taking or a lack of "experiencing" another's visual perception.

Povinelli and colleagues studied the ability of chimpanzees (Povinelli, Nelson and Boysen 1990, 1992, Povinelli, Rulf and Bierschwale 1994) and rhesus monkeys (Povinelli, Parks and Novak 1991, 1992) to appreciate another's visual perspective and assess levels of knowledge or absence of knowledge based on visual perception. Subjects were required to use their appreciation of another's perspective to reverse roles. The same apparatus was used for chimpanzee and rhesus monkey subjects. The apparatus consisted of two (or eight) opaque shielded food trays attached to each other by a complicated series of spring joints which allowed the trays to be moved apart to both ends of the apparatus, when a handle was pulled at one end of the apparatus (see Figure 7.1).

The subjects were trained to pull the handle, which delivered food to both ends of the apparatus within reach of the subjects and a human experimenter. The subject pulling the handle could not see the presence of the food on a tray and was called the *operator*. The experimenter who could see the food was named the *informant*. The subjects were initially trained to pull the handle corresponding to the tray which a human experimenter baited within the subject's view. In the next phase, the subjects were paired with a human experimenter. The subjects were then split into two groups, operators and informants. The primate informants had to watch an unknown human experimenter bait one food tray, whilst the paired experimenter (operator) was not present. The subjects then had to gesture towards the baited tray. In the second group, primate operators, had to respond correctly to the cues provided by the human informant, by pulling the handle corresponding to the tray which the human informant pointed at. The last phase of the experiment required that the primate subjects reversed roles with human experimenters, i.e. the primate informants became operators and visa versa.

Chimpanzee subjects responded correctly as informants and operators respectively and there was a clear transfer of roles in the last experimental phase (Povinelli, Nelson and Boysen 1992). It would appear that the chimpanzees understand

Figure 7.1. Diagrammatic representation of apparatus used to test role-reversal and attribution of knowledge in others, in experiments with rhesus macaques and chimpanzees (Povinelli, Nelson and Boysen 1990, 1992, Povinelli, Parks and Novak 1991, 1992). The opaque shields prevent the operators from seeing which food tray has been baited.



pointing as referential communication and could easily reverse role. Rhesus macaques responded differently to the chimpanzees (Povinelli, Parks and Novak 1992). The monkey operators were able to use pointing cues to receive food rewards, but could not transfer to unknown roles. This is evidence that rhesus monkeys can not appreciate another's visual perspective. Monkey informants made reaching/pulling motions towards the food which the human observers could interpret correctly. Povinelli has suggested that the monkeys were not responding to pointing gestures in a communicative way, but were actually trying to reach the food themselves. When the roles were reversed, the informants responded at chance level. The operators performed poorly at first, but then steadily improved. Operators can, therefore learn to become informants.

In guessing versus knowing experiments, the same apparatus was used as in the role reversal experiments. Again, the subjects learnt to point to the correctly baited tray and learned to respond to similar pointing cues from a human experimenter. In this experiment, however, the subjects had two choices of human informant (guesser and knower). The knower baited the food tray whilst the guesser was out of the room. When the guesser re-entered the room, both experimenters pointed at a tray; the knower towards the baited tray. The subject had to respond by pulling the handle indicated by the knower (and the baited tray). Cues to help with reinforcing the identity of the knower were added in later phases of the experiment, such as a red or blue hat. In the transfer phase, the guesser and knower both remained in the laboratory whilst a third experimenter baited the food trays. At this time, the guesser placed a bag over his own head, obstructing his view of the baiting procedure. All chimpanzee subjects responded significantly more to the signals provided by the knower than the guesser in all phases, including the bag over head phase (Povinelli, Nelson and Boysen 1990).

The rhesus monkey subjects had an additional testing phase where the knower wore a pink glove when pointing to the baited tray. This additional cue did not seem to help the monkeys, as they did not seem to discriminate between the guesser and the knower in any phases of this experiment (Povinelli, Parks and Novak 1991).

The experiments described above suggest that great apes, but not other non-human primates process other's gaze within a purposive behaviourist framework. A

behaviourist interpretation would suggest that non-human primates respond to attention cues in terms of reward and learning about stimulus-response relationships. For example, "X follows the gaze of Y as X has learnt that nutritious fruit attracts Y's gaze". X will be rewarded (i.e. will have access to fruit) if X responds appropriately after observing Y's gaze. A purposive behaviour interpretation of the above experiments require that the monkeys and apes understand that other individuals of their own or other species perform acts for a specific purpose. A leopard hunts monkeys because it has to eat, a chimpanzee looks at a patch of fruit because he intends to eat the fruit, etc. Difficulties in interpretation arise, not just when suggesting that others have purpose in their behaviour, but also when suggesting that individuals can interpret and understand another's purpose from behaviour patterns.

Anecdotes and observational studies described above, for monkeys in their natural habitat, suggest that monkeys and great apes do understand the meaning behind the gaze and attention of others. Experimental studies performed in the laboratory, however, suggest a dichotomy between the abilities of monkeys and apes in utilising social attention information. Great apes, such as chimpanzees and gorillas do appear to use the direction of another's attention to interpret another's intentions (as related to objects in the world). There appears to be no evidence that monkeys utilise social attention cues in the same manner as the great apes, when tested in the laboratory. The dichotomy may arise between an apparent positive ability in feral-ranging monkeys and an apparent negative ability in laboratory monkeys, because the social attention cues presented in the monkey's natural environment would have been provided by conspecifics. Social attention cues in the laboratory would have been provided by human experimenters. The great apes may have the ability to use non-ape social attention cues, whereas monkeys may only utilise conspecific cues (see Chapter IX for behavioural data which suggest that this may be the case for gaze following in monkeys).

(b) Intentional motion

The classic studies of primate's perception of purposive (or intentional) motion were performed by Menzel (Menzel 1971, 1973, 1974, 1979, Menzel and Halpein 1975).

A mixed group of juvenile chimpanzees was allowed to move freely around a semi-natural environment (a one-acre "naturalistic" cage, with trees and shrubs) which could be easily manipulated by the experimenters. Before releasing the chimpanzees, the experimenters hid pieces of fruit and novel objects, such as toys with one chimpanzee present. (Usually the experimenters chose a subject who was unperturbed when being handled, and they would physically show the chimpanzee the position of the hidden object, or hide it in front of the chimpanzee.) The subject (named the "leader") was then taken back to his/her home cage and released with the other members of the group into the enclosure.

The rationale of this experiment was to test whether other members of the chimpanzee group would be able to infer the location of the hidden objects from the leader's behaviour (direction and movement cues) and whether such cues could be used to transmit other forms of information about the hidden objects, such as the objects' presence, quality and amount (Menzel 1971).

When a large amount of food was hidden (six pieces of fruit), the other subjects followed closely and occasionally attempted to move ahead of the leader. The followers appeared to be projecting a trajectory from the orientation and motion direction of the leader to a point in space where the fruit may have been hidden.

When the experimenters changed the nature of the objects (the leaders were shown a plastic snake or alligator compared to fruit or a pile leaves) the followers approached the "frightening" objects with caution. The subjects were also cautious when approaching positions where they presumed frightening objects were present (the experimenters removed the frightening objects after showing the object's position to the leader). Thus, the leader appears to have communicated the valence and location of objects.

A further experiment looked at the communication about the presence versus absence of objects. The experimenters hid large amounts of fruit as usual, but also provided some small amounts of visible food attached to a stake. The subjects tended to follow the leader to the hidden fruit, rather than the lesser amount of visible food. Communication about the quality of hidden food was also studied. Two leaders were

each shown one pile of food (fruit or vegetables). In 80% of trials the subjects followed the leader making towards the fruit (higher quality food). What forms of signals were the leaders and followers using to communicate such a wide body of information? Menzel stated that no specialised vocalisations, hand or limb gestures or facial expressions were noted in any of the trials, but the leader would "get up, orient and move independently in a consistent direction, as if he knew exactly where he was going and why" (Menzel 1971, p. 228). It therefore appears that chimpanzees, at least, can use simple behavioural cues, such as direction of attention, and motion and speed as indicators of others intention (to get nice food).

The same experiment has been replicated for mangabeys (Coussi-Korbel 1994), and a similar pattern of results to those of Menzel were found. The majority of group members who had not seen the hiding of the food followed the informed individual on 53% of trials. Differences in behaviour were attributed to social dominance and deception. A submissive "leader" who was shown the food would not go straight to the food when the dominant male was present, but would either wait or take an indirect food to take it when the dominant's attention was elsewhere.

It is probable that other primates use similar attention or motion cues to learn about objects in the environment from conspecifics. One example, may be the daily march of hamadryas baboons. Kummer (1995) reported that the hamadryas baboons of Ethiopia move from large groups on "sleeping rocks" (or cliff faces) in the morning and split, first into bands, then into smaller clans and finally into family groups (comprising one male, the male's harem of females and infants). The bands tend to move away in different directions, but the clans stay relatively close to one another. An ability to know the identity of the individual members of a clan, an ability to interpret the actions of the alpha male and an ability to determine the direction of the alpha male's movement, may all be important for successful and speedy clan movement. The members of a clan may use visual (direction of movement, attention direction, etc.) and vocal signals from the leader and the leader's cohorts to influence the direction of the group move. It may also be important for the members of one clan to notice the direction in which another clan moves, to predict where they intend to travel and the final destination, therefore avoiding

meeting them at a feeding place or drinking hole which may only be able to sustain one clan. Multiple clans form into bands again at a sleeping rock in the evening.

Other forms of primate motor behaviour have been described using communicative or mentalistic terminology. Bertrand (1969) discussed the "dominant walk" of stumptailed macaques; the slow, deliberate walk where the (usually dominant adult male) monkey looks directly ahead, with its tail raised. Bertrand (1969, p. 57) "had the impression that an alpha male purposefully maintained a slow walk, whereas other animals tended to run". This same form of motion was also noted in rhesus and Japanese macaques, by the same author (Bertrand 1969). Other such forms of dominant walk have been identified in a range of primates; the "swaggering walk" of *Lemur catta*, the "confident gait" of olive baboons, the "confident walk" of vervets, the "strutting walk" of gorillas and the "powerful, measured gait" of langurs (Quotations from Bertrand 1969, p. 57). These examples suggest that the manner of walking may be a good indicator of dominance status (i.e. a dominant animal walks confidently, but with an arched back, whereas a subordinate animal nervously runs to avoid social interaction).

Bertrand also discussed two other forms of macaque motion, which may have a communicative function. First, submissive animals would often move slowly, whilst sitting down, usually towards a food source monopolised by a dominant animal. The submissive monkey would shift along the ground to the food and take some if tolerated by the dominant. The second was the so-called "follow-me walk", similar to the dominant walk, as the monkey walks deliberately in one direction, but they also glance back at the individual they want to follow them. This behaviour was also noted for rhesus, Japanese, lion-tailed and barbary macaques (Bertrand 1969, personal observations), hamadryas baboons (Kummer 1968) and gorillas (Schaller 1964). The first example could be an attempt by the subordinate monkey to suggest to the more dominant animal that it is not a threat. The second example may be an example of referential communication, directing another's attention onto an interesting object. (This interpretation would require the monkey to understand gaze as a means of communication, with subjects using similar abilities to those used in the experiment described above with a gorilla, Gomez 1990, 1991.)

This section described experiments which suggest that a number of monkeys and apes may understand that others move (whole body or limbs) for a purpose. The purpose of the behaviour can be as simple as to get from A to B. Menzel's experiments suggest that chimpanzees (at least) use direction of motion cues to locate hidden objects and the quality of the objects (food, predator, etc.). Some non-human primates may therefore use gaze direction and direction of motion cues to learn about objects in the world and more specifically how others intend to interact with those objects. The next section discusses experiments of social learning and imitation (or learning about others interactions with objects), which may link the propositions made in the first two sections.

(d) Social learning, imitation and tool use.

Social learning may be defined as learning something about objects, events and actions in the world from social interaction with conspecifics (however, vervets appear to learn from others species, e.g. the specific alarm calls of starlings, Seyfarth and Cheney 1990). There are many forms of behaviour that require learning from conspecifics which may be called social learning (Whiten and Ham 1992, Byrne and Russon 1997).

Stimulus enhancement (SE) is where individual X interacts with an object and the observing animal, Y's attention is drawn to the object because of the interaction. Local enhancement (LE) is a related phenomenon. Individual X is located in a particular area. Y's attention is drawn to the sama area, because of X's location within that area. For example, individual X is standing next to a tree with abundant fruit. Individual Y becomes attracted to the tree because X is located next to the tree.

Observational conditioning is a form of social learning about objects and events. A previously neutral stimulus becomes aversive, frightening, pleasant, etc. due to the reactions and interactions of individual X with the previously neutral stimulus (object, event or action). Individual Y learns about the presence and location of objects, as with SE and LE, but also about the significance of the objects. Whiten and Ham (1992) also suggest that Y learns from X *to what* it should direct actions already within its repertoire. An example, is observational conditioning of snake fear. Laboratory raised rhesus monkeys are not naturally fearful of snakes (Mineka et al 1980), but can be conditioned

to become fearful of real, fake and toy snakes when in the presence of naturally fearful wild-born parents, directing fearful expressions towards the snakes (Mineka et al 1984).

Imitation or "monkey-see-monkey-do" or "to ape" is a not the simple form of behaviour that is depicted in popular human culture. To some extent, imitation includes SE and LE, but individual Y must also learn some aspect of the intrinsic form of an action from individual X (Whiten and Ham 1992). A strict criteria for imitation, is copying a sequence of actions from a demonstrator which are novel (i.e. are not within the behavioural repertoire of the observing animal), but available for inclusion in the behavioural repertoire, which are used to achieve the same goal as the demonstrator's action (Byrne and Russon 1997). For example, a chimpanzee may have the physical capabilities to use a knife and fork (i.e. the correct grip and motor control). Using a knife and fork, however, would be a novel action for chimpanzees. A successful example of imitation, using the criteria above, would be as follows. A chimpanzee would watch a demonstrator picking up a knife and fork in either hand and cutting a piece of fruit in half. The chimpanzee would then be required to pick up the knife and fork in the correct hands and cut the fruit in the same manner as was observed.

Finally, goal-emulation (Tomasello 1990) is a form of social learning, where a goal-directed sequence of action is not copied precisely, but the final goal of the action is. Tomasello et al (1987) studied the responses of chimpanzees watching actors using a rake to collect out of reach food. The method demonstrated was to turn the rake over to the straight edged-side and pull in the food, rather than keep the rake serrated side down and hope that the food does not slip through the serations in the rake. The subjects did not copy the specific actions (flip over to serrated side and pull) but achieved the goal (reaching and pulling in the food) on a large number of occasions. Tomasello et al (1987) concluded that as the final goal was achieved, but the actions used to achieve the goal were not copied, the method of social learning which the chimpanzees used was emulation.

The ability to determine the focus or object of another's attention is vitally important for social learning. Actions may be directed onto objects (which may be tools, food, conspecifics or parts of the body). The capacity to learn about objects by observing

other's interactions with objects requires that the observing individual's attention is drawn to the correct object. Nothing can be learnt about one specific object, if attention is directed to another, unrelated object.

The presence of imitative ability in monkeys and apes is a highly contentious issue. All textbook examples of monkey imitative learning have now been reasonably explained by other forms of social learning. Japanese macaque potato washing has been presumed to be due to imitation, which is a relatively rapid form of social learning (the behaviour is modelled then replicated). Yet, potato washing was found to be acquired over long lengths of time (mean 2 years, Whiten and Ham 1992). Potato-washing, due to length of time to acquire the behaviour, has been suggested to be a part of Japanese macaque culture, other examples being wheat-washing, fish-eating and stone-handling (Huffman 1996). Culture has been defined by Imanishi in 1952 as "socially transmitted adjustable behavior" (Nishida 1987, p. 462). In the case of potato-washing, the initial ability may have been acquired through individual learning (trial and error). The behaviour would then have been observed by other individuals, who would have had the opportunity to learn to perform the action of potato-washing over time. The term culture suggests that the potato-washing ability would be acquired over time and would be passed from generation to generation (i.e. the ability would still be displayed in animals present generations after the initial manifestation of the ability). Cultural learning, therefore is a form of social learning, dependent on long-term learning processes, not just learning independent actions (or sequences of actions) within a short time-scale (Tomasello, Kruger and Ratner 1993).

There may be simple reasons why monkeys fail on most studies of imitation, compared to studies of other forms of social learning (Hall 1963, Whiten and Ham 1992). First, monkeys do not appear to be efficient tool users (in natural and captive environments). Second, in experimental studies, humans provide the actions to be imitated. Visalberghi and Fragaszy (1990) described experiments where capuchin monkeys (the most proficient primate tool users after chimpanzees) were presented with shelled nuts and stones or blocks of wood which could be used to crack open the nuts. They tested the ability of capuchins to use the stones or blocks of wood as tools to crack

open the nuts. One capuchin was proficient at this and would demonstrate the nut-cracking behaviour many times in front of observers. The ability to crack open nuts did not transmit through to the observers. A second experiment also demonstrated a basic lack of imitative skills in tool use. Capuchin subjects were presented with a transparent tube, which was baited with food in the centre. The subjects were given sticks of sufficient length to poke the food through the tube. Three out of four subjects achieved this, but the fourth did not, even when given the opportunity to watch proficient modellers for a total of 3.5 hours. The fourth subject did not learn either by trial and error, or by other forms of social learning (including imitation).

One other study tested the ability of non-human primates to imitate the actions of a conspecific (Thrumble 1987, Thrumble and Perrett 1987). The results of the study provided evidence that some stumptailed macaques could use tools in similar ways to capuchins, but did not learn how to use tools from a proficient conspecific (i.e. the observing subjects used individual learning rather than imitation). Non-proficient subjects did not learn from conspecifics, even though the subjects were presented with 300 hours of time to observe modellers (Perrett, personal communication).

The use of the popular term "monkey see, monkey do", appears to be a little strained. There is little or no evidence of monkey imitation. A second popular term is "to ape". Tomasello (amongst others, 1996) has asked the question "do apes ape?". Only two very recent studies could be said to be indicative of some form of imitation. Whiten et al (1996) looked at whether chimpanzees and human children imitate novel actions on novel objects (which Whiten et al called artificial fruit). The artificial fruit were constructed so as to pose food-processing problems which chimpanzees would encounter during normal feeding behaviour. Two actions in sequence were required to open the artificial fruit, requiring not only goal-emulation (the ultimate goal of opening the artificial fruit) but also imitation, using the correct observed actions. The actions were complex and consisted of multiple parts (e.g. twist barrel whilst pulling out). The children were fairly proficient imitators of all observed actions, whereas the chimpanzee subjects were only proficient in copying one of the two actions (there were individual differences in which action was copied).

A second study may be indicative of imitation skills in chimpanzees. Custance et al (1995) replicated a study by Hayes and Hayes (1952). Language-trained chimpanzee subjects were taught to copy a series of gestures on command of "do this!" (the experimenter gained the subject's attention, then performed the action). The ability to copy actions was then transferred to 48 novel actions. Two subjects correctly imitated 13 and 17 out of the 48 novel actions respectively. Examples of such arbitrary (non-functional) actions were wiggle fingers, wobble lips, clap back of hand. It is contentious whether these actions test for copying or imitation; they do not test for goal directed actions on objects in the world.

Actions directed towards a goal object (meaning an object external to the body; such as a tool), may not be part of the dependent criteria for imitation. For example, imitating an individual playing with their hair, or an individual lifting one arm with the other arm would be examples of actions directed towards objects, not external to the body. Meltzoff and Moore (1977) tested the ability of human neonates to imitate facial and body gestures, such as tongue poking and hand waving.

Imitation requires the analysis of another's viewpoint or visual perspective (Whiten 1996) and a visuomotor transformation from a visual representation (observed action) to a motor representation (performed action). The next section discusses recent neurophysiological data which may provide evidence that single neurons in premotor cortex are capable of visuomotor transformations which would be required for imitation.

7.1.2 Neurophysiology of Perceiving Purposive Behaviour

The behavioural examples reported above suggest that learning about another's behaviour and intentions can be computed from basic perceptual signals. The studies described in this section provide some evidence that particular neural sub-systems exist in the monkey brain for the analysis of other's purposive behaviour.

(a) Social attention

The brain of the rhesus monkey contains neurons which respond preferentially to the sight of human or monkey faces (Bruce et al. 1981, Perrett et al. 1982, Desimone et al. 1984). An important first step in social interaction is recognition of a second individual (see Chapter VIII). Cells with responses selective for faces over other objects have been found in the upper and lower banks and the fundus of the superior temporal sulcus (STS), in an area named the superior temporal polysensory area (STPa). This region contains cells which respond to polymodal stimuli (visual, auditory and tactile, Bruce et al 1981). Perrett et al (1982) recorded from cells in the fundus of the STS and found that the responses of face selective neurons were not affected by transformations of the face (changing colour, size, vertical orientation). Scrambling the features of the face did reduce the cells' responses. Separating the face into component parts (eyes, nose, mouth, etc.) and presenting the separate part without the other parts reduced the response of some cells from the initial strong response to the whole face. Some cells, however, responded equally well when the eyes or the mouth region were presented alone.

Importantly, rotating the face horizontally away from the front view also changed the response of a number of cells (21/32 cells). It therefore appeared from this study that the presence of the eyes and the head view were important for a number of cells. An increase in response was seen with one cell, when the face was presented in profile. These findings were extended. Perrett et al (1985b) found that view had a dramatic effect on the responses of face responsive neurons. Some cells were tuned to the face, with a gradual decline in response with increasing horizontal rotation from the face. Other cells produced opposite responses, where the cell was preferentially responsive to a profile (e.g. left profile) with a decline in response as the head was rotated towards the face view (view 0^0). Elevation of the head appeared to effect cell responses (some cells preferred heads that were level, other cells preferred heads that were facing upwards. A large number of cells were responsive to all views of the head (non-selective for view). Eye gaze was also important. Sixty-four percent of cells selective for the face and profile were also dependent on the position of the eyes. The majority of cells preferred that the

head and eyes were in compatible directions with respect to the viewer, e.g. head left and eyes left. Some cells were selective for eye position independent of the head view. For example, the response to head left and eyes facing viewer would be the same as head and eyes facing the viewer, or head right and eyes facing the viewer. Eye gaze dependent cells often did not require the presence of the rest of the head to respond. Other cells were only responsive when the eyes were averted from the viewer. This is important behaviourally for macaques, as direct eye contact is a threat (see Chapter IX).

In a later study, Perrett et al (1991) classified the responses of head selective neurons into two forms of coding (object-centred and viewer-centred, see also Hasselmo et al 1989). Object-centred coding would seem an appropriate label for neurons which do not discriminate head view (i.e. all views of the head are equally responsive). Any view of the head is sufficient for object recognition, such as object X is a head. Cells responsive to multiple views of the head may be responsive to features common to all views, such as hair or an ear. Recognition may only require the analysis of four "characteristic" views of the head (face, left and right profiles and back of the head). Object-centred coding requires independent analysis of at least these four views. Object-centred cells may be combining the outputs of viewer-centred cells. The term "viewer-centred coding" is applied to neurons which are selective to one or more, but not all views. Usually, the sight of only one view causes the cell to be maximally responsive. Cells selective for view were either narrowly-tuned (only the presentation of one view was sufficient for maximal firing from the cell) or broadly-tuned (one view was sufficient for firing, but the cell response declined as the head was horizontally rotated further from the view providing the maximal cell response). Cells broadly-tuned to view would only require tuning within (+/-) 45^0 of the four characteristic views to code for all views (360^0) of the head. Only four broadly-tuned viewer-centred cells, therefore, are required to code for all possible views in the horizontal plane.

Perrett et al found that object-centred neurons were rare (4/119 cells tested), whereas the majority of cells were responsive to one view (99/110 cells). A numbers of viewer-centred cells were responsive to views which were not one of the four characteristic views. This suggested to Perrett et al (1991) that the function of these

neurons (and neurons with responses selective for one of the four characteristic views) may be to determine the direction of another's attention, as these cells were superfluous to requirements for face recognition.

The breadth of tuning exhibited by some viewer-centred neurons would not explain cell responses to vertical head elevation. Perrett et al (1985b) found that a number of cells were unresponsive to changes in horizontal orientations of the head, but were affected by vertical elevation. For example, a cell may have responded to all frontal, horizontal views, but only when the head was directed upwards i.e. head 45^0, up had the same response as head view 90^0, up and head view 0^0, up. Other cells were dependent on the view and elevation of the head, i.e. head view 0^0, up compared with head view 0^0, down.

Perrett et al (1992) reported the activity of a cell responsive to attention down. The cell was responsive when the head was directed down, the eyes were directed down or the head and body posture (quadrupedal) was directed downwards. Changing the elevation of the eyes in relation to the head (e.g. eyes directed towards the viewer, head downwards) and the head in relation to the body (e.g. head directed at the viewer, but body posture downwards) would change the direction of attention. Head elevation, therefore, is also an important indicator of attention direction. For example, attention to the left (horizontal, level head) is different to attention up and left or attention down and left.

A large number of cells sensitive to the horizontal head view were also sensitive to the position of the eyes. Perrett et al (1985b) found that a number of cells responsive to the face (directed towards the viewer) preferred that the eyes were also directed towards the viewer. Similarly, if a cell was responsive to the head view 45^0 (half profile), the cell preferred that the eyes were also averted to 45^0 from the viewer. Some cells responsive to the face were insensitive to the position of the eyes, i.e. there was no difference in response between eye contact and eyes averted.

Previous studies have suggest that the eyes are ultimately important for recognising another's direction of attention (Perrett et al 1990d, Perrett et al 1992). It is possible that if the eyes become occluded from view (for example, under poor lighting

conditions; Hietanen et al 1992), information from the head becomes important. In a similar manner, cells responsive to the information provided from the body will become important if the head is occluded from view, Perrett et al (1992) proposed that the information provided by eye/face/body sensitive neurons was part of a processing hierarchy (for attention direction or *social attention*).

Most cells within the STS were responsive to heads, but 42% (of 53 cells tested) were also responsive to information from the rest of the body (Wachsmuth et al 1994). Wachsmuth et al (1994) tested the response of cells to the presentation of the head only (with the body occluded), the body only (with head occluded) or the whole body (head and body). Ninety percent of cells responsive to the head and body were dependent on view (usually the head and body were presented in compatible directions). Body view may be an indicator of attention direction (when the head and eyes are not present or occluded). If the head is also present, however, then the information provided by the body will be superceded by information from the head. For example, the body may be oriented towards the viewer, but the head is directed to the right. Attention direction would be determined to be towards the right. The position of the eyes may be a more important indicator of attention direction than the head and body (see behavioural studies described in Chapter IX), so information from the eyes may inhibit information from the head. Perrett et al (1992) proposed this when discussing a cell responsive to attention down (see earlier). The cell was responsive to the eyes, head and body directed downwards. When the cell was presented with body down, but head up (profile), the response was reduced from the response to head down body down. A critical test would have been head down, eyes directed towards the viewer. If the response of the cell was to attention down, the predicted response would be a decrease, as attention would now be attention towards the viewer (if position of the eyes are more important then head direction). Unfortunately, this was not tested.

Physiological responses to eye gaze have been found in other brain regions. Brothers (Brothers et al. 1990, Brothers and Ring 1993) recorded from single cells in the amygdala (accessory basal, lateral basal, medial basal, cortical and central nuclei) and rhinal sulcus. Brothers found that two cells were responsive when a video-stimulus of a

stump-tailed macaque looked directly into the camera (i.e. eyes directed towards the viewer), but not when the video-stimulus averted gaze away from the viewer.

Further evidence suggests that the STPa and probably amygdala and rhinal sulcus form part of a system coding the direction of another's attention (eye gaze direction, not just gaze away or towards a viewer). Campbell et al (1990) and Heywood and Cowey (1992), lesioned the STS (including STPa) after testing the limits of eye gaze discrimination in rhesus monkeys. Pre-operatively, the monkeys had to perform a two-choice picture task and to choose the picture with the eyes averted. Differing degrees of eye gaze displacement (head view 0^0), from eye gaze aversion to eye contact were presented (5^0, 10^0 or 20^0 degrees deviation from view 0^0). The eyes and head were varied independently (e.g. head view 20^0 from 0^0, eyes 10^0 from 0^0), to determine whether the monkeys were using eye gaze rather than head position as a discriminative cue. Before surgery, the monkeys were extremely good (75-90% correct) at discriminations of gaze directions, 10^0 and 20^0 from 0^0, but poor (chance) at 5^0 from 0^0. After removal of the STS, the monkeys performance at discriminations of gaze directions, 10^0 and 20^0 from 0^0, was reduced to 50-60% (approximately chance level). It would therefore appear that rhesus monkeys can discriminate gaze averted laterally from eye contact (10^0 and 20^0 from 0^0) and that the STS is important for these discriminations.

Eacott et al (1993) also tested the ability of rhesus monkeys with lesions of the STS to discriminate gaze. Pairs of eyes (without the head) were presented towards the viewing monkeys (0^0) or averted at deviations of 5^0, 10^0, 15^0 or 20^0 from the viewer. Although the head was occluded, the eyes were presented as part of a head either directed towards the viewer, or averted (20^0 to the left or right of the viewer). The subjects were presented with a two-choice discrimination, choosing between eyes directed towards the viewer (incorrect stimulus) versus eyes averted (correct stimulus), irrespective of the position of the head. The unoperated animals were better (overall) at discriminations of eye gaze (deviation > 5^0) than the STS lesioned animals. Although, both groups of subjects were the same at discriminations of 5^0 from the viewer, the choices were significantly greater than from chance. The percentage number of correct choices increased with increasing deviation from the viewer. Lesioned animals were also

impaired on a novel two-choice discrimination task (between different groups of ASCII characters). Eacott et al (1993) thus concluded that the deficits in processing differences in eye gaze were due to deficits in two-choice discrimination learning. There have been no suggestions that the STS is a region which solely processes information about gaze. Gaze directed towards the viewer may be an exemplar, which may be compared with other instances of gaze. This may be why there is no difference between operated and unoperated subjects in discriminating gaze deviations of 5^0 from the viewer. The eye position would not be sufficiently different from the exemplar to aid discrimination. Eacott et al (1993) failed to test the monkey subjects on eye gaze discrimination before STS surgery. It is not known how the operated subjects would have performed pre-operatively in the discrimination task.

(b) Intentional motion and imitation

Simple motion cues are processed in the extrastriate areas of the macaque temporal lobe. Areas MT (middle temporal cortex), MST (middle superior temporal cortex), FST (fundus of the superior temporal cortex), A7a (posterior parietal area)and VIP (ventral intraparietal area) are the areas of the extrastriate cortex which appear to be involved in the simple analysis of motion. Literature on the cellular processing of simple motion cues is extensive and largely irrelevant to the discussion here (see Hildreth and Koch 1987, Maunsell and Newsome 1987, Newsome et al 1990 for reviews).

Processing of the motion of complex objects occurs further away from primary visual cortex and prestriate areas (MT, FST, etc.) in the superior temporal polysensory area (STPa, Oram et al 1993). Some cells in this region code for the form of an object in motion, whereas other cells in this region are unselective for the form of the object, but are sensitive to the direction of motion. These cells may be derived from direction specific cells found in MT and MST, as there are distinct projections from the middle temporal areas in the STS (MT, MST and FST) to the more anterior part of the STS (STPa, Boussaoud et al 1990).

A large number of cells within STPa respond to the specific motion of complex objects, responding to motion in a particular direction, with a particular form (i.e. a

walking human body) and a specific view (i.e. compatible with the motion direction (i.e. "following the nose"). Perrett et al (1985a) were the first to report the responses of cells to whole body motion (i.e. walking). Cells sensitive to motion stimuli had latencies equivalent to cells sensitive to static stimuli. The majority of cells were responsive to the motion of a body (translation) in one preferred direction (i.e. walk left to right) and some cells were responsive to translation in two directions (180^0 apart, i.e. walk towards and away from the monkey). The cells did not appear to discriminate between the velocity of motion (20-120 deg/sec), although changing the velocity during motion did effect the responses of some cells. A small number of cells were insensitive to the form of the object in motion (i.e. responded equally to walking bodies and control objects moving in the same direction). Some cells were only responsive when the translation of the body was out of or into view, but equally responsive when a screen was passed in front of a static body. Cells within this brain region were also sensitive to body rotation (i.e. facing the monkey to facing away from the monkey in one motion), limb and body part articulation.

Perrett et al (1985a) found that the response of neurons sensitive to body motion were dependent on the direction of motion (i.e. walk left to right, not right to left). The majority of cells required that the view of the body was compatible to the preferred direction of motion (i.e. walk left, facing left). A small number of cells which responded to one direction of motion, were broadly tuned to view, i.e. were responsive to two views, 180^0 apart, moving in one direction). For example, a cell may be responsive to walk towards the monkey, but responses to views 0^0 (facing the monkey) and 180^0 (facing away from the monkey) would be equal.

Johansson (1973) termed motion where a very small amount of form was present but no distinguishing features, as "biological motion". Biological motion stimuli consist of lights attached to the body at joints and positions along the limbs and torso. Human subjects were clearly able to discriminate that these lights represented people walking. Oram and Perrett (1994) found that 25% of cells tested for whole body motion in the upper bank and fundus of the STS (Seltzer and Pandya 1978) were responsive to biological motion stimuli (human stimuli with lights on the limbs). The large majority of

cells selective for body motion found in this highly complex processing area were selective for the form and motion of complex objects, such as walking bodies, with articulating limbs (Perrett et al 1985a, Oram and Perrett 1996).

The majority of form selective cells within this region were also sensitive for the direction of motion (i.e. walk left, Oram and Perrett 1996). Seventy-eight percent (125/161) of these cells also required that the body view was compatible to the direction of travel (e.g. walk left facing left). Oram and Perrett (1996) found that 5% of cells were broadly tuned for view (two views 180^0 apart, one direction of motion) and 2% were non-selective for direction of motion (i.e. responsive to any direction), but required that view was compatible with the direction of motion. A few cells were responsive to incompatible motion (i.e. walk left, facing right). Oram and Perrett (1996) found that the latency of cells selective for motion information, but not form were responding 20msec earlier than cells responsive to form information only. The latencies of cells responsive to form and motion information were the same as cells responsive to motion direction only and the latencies of cells responsive to direction were 35msec earlier than cells responsive to form information. Oram and Perrett suggested that cells with longer latencies showed more form sensitivity, so motion information is processed before form information.

A subpopulation of cells in STPa respond to the sight of movements of different parts of the body (Perrett et al 1985a, Oram et al, submitted), such as the limbs (arms and legs), smaller units of limbs (such as hands and fingers), shoulders, heads and torsos (as components of whole body motion). The responses of the majority of cells were not dependent that the limbs were attached to the body (i.e. independent movement was sufficient for responses).

Perrett et al (1989a, b, 1990a) studied the responses of neurons in the lower bank of the STS (TEa) to hand actions. All cells reported required that the hand actions were directed towards objects. Seven different actions were categorised (reach, retrieve, manipulate, pick, tear, present to monkey and hold). Although some cells were responsive only to the sight of one action, some cells did respond to two or more actions (although not all). The vast majority (92%) of cells were unselective for the view of the actions, i.e. the cells were equally responsive to the front and the profile views of the

actions. The interaction between the hand and objects appeared to be important to the neural responses. Perrett et al (1989a) suggested that viewer- and object-centred coding was insufficient to describe the coding of these neurons. Perrett et al (1989a) termed the coding of actions performed onto objects (or specific locations) as goal-centred coding:

"we define goal-centred descriptions as descriptions in which the disposition or movements of one animate object (the agent) are specified with respect to a second object or part of the environment (the goal)." (p.101).

The responses of cells sensitive to hand actions were unselective for the object (or goal), however, some cells preferred deformable objects and some cells preferred foods over non-foods. The size of the object was also unimportant. The interaction between hand and object was ultimately important, as the motion of hands without an object, the object moving without the presence of hands or the hands and object moving but spatially separated did not cause the cell to respond (Perrett et al 1989a, b).

Reaching to objects in particular locations relative to the viewer were more important than reaching to different locations with no object as a goal. For example, a cell was responsive to the sight of reaching to an object to the left of the monkey. The cell did not respond to reaching to the right of the monkey, where there was no object present. Reaching *per se* was not important, but reaching to a particular object, only located to the left of the monkey was important. Moving the monkey, so that the object was positioned to the right of the monkey may not have reduced the response of the cell.

The interaction between animate and inanimate objects was highlighted with cells responsive to the sight of the experimenter bringing food to their mouth. The cell was responsive to the food moving towards the mouth or the mouth moving towards the food. There is an interaction, but the cell appears to be responsive to two different types of movement achieving the same goal.

Goal-centred coding was also apparent in the responses of some neurons sensitive to whole body motion. Perrett et al (1990a, b) reported a cell which was maximally responsive when an experimenter walked towards the laboratory door (to the right of the monkey). The monkey was positioned towards the facing wall. The response of the cell

was not dependent on the initial starting position (i.e. left or right of the door or in front of the monkey), the cell only responded when the final destination of travel was the door. The response was not affected by positioning the monkey towards the door and again walking towards the door.

Studies in humans using neuroimaging techniques (PET) have confirmed the results seen with monkeys, that the rostral STS and amygdala are activated when human subjects watch biological motion displays of expressive motion, such as dancing (Bonda et al 1996). Bonda et al (1996) found activation in human caudal STS (and intraparietal sulcus) when subjects viewed light-point displays attached to reaching and grasping arms.

PET studies using human subjects indicate that similar regions of the human neocortex are responsive for coding the sight and motor responses of actions. Rizzolatti et al (1996b) found that the following regions showed significant levels of activation when subjects watched grasping actions (frontal gyrus; A8, A7, A45, middle occipital gyrus, A19/37). Object prehension (grasping objects by the subjects) caused significant activation in the following areas (precentral and mesial motor areas, putamen, cerebellum, superior parietal lobule, cuneus, cingulate gyrus; A24, inferior parietal lobule; A40, A1, A2, A3, A4 and precuneus; A7). There appear to be similarities between the location of coding the visual appearance and the motor component of actions (A8).

The motor cortex of normal human subjects was magnetically stimulated whilst the subjects watched an experimenter reaching for objects, the objects alone and the experimenter tracing figures in the air (Fadiga et al 1995). Motor evoked potentials (MEPs) were measured in four muscles from the hand during observation. Fadiga et al found that significant increases in MEPs were correlated with observing the actions, with similar levels of activity seen in the muscles when the same actions were performed.

The importance of coding the specific direction of another's whole body and body part motion from the viewpoint of reading intentions is relatively clear. As described previously, monkeys and apes appear to infer purpose from complex motion (such as walking), view (attention direction) and direction of motion (e.g. move left) cues. A neural system which can process such details quickly is ultimately going to be of benefit to observing animals. For example, knowing that a dominant individual is moving quickly

towards an observer rather than towards an individual next to the observer, may allow an appropriate response to be prepared. This has important implications if the approaching animal is a predator. An animal approaching slowly is unlikely to be a predator or aggressive animal (unless hidden in undergrowth). A stimulus approaching quickly, however, is likely to be dangerous. Perrett et al 91989a) reported that neuronal responses did not discriminate between fast and slow motion, however changes in velocity did effect some responses. Information connected with a fast approaching stimulus may be processed using non-form selective cues, such as speed of approach, rather than more complex processing of form such as "object X is a leopard".

Neural coding of limb and extremity movements is important for imitation and social learning. Of greater importance, however, is the relationship between moving limbs, extremities, whole bodies, etc. and objects in the environment (such as reaching to a piece of fruit, see Menzel's experiments detailed earlier).

Neural mechanisms responsive to other's manipulation of objects therefore appear to be present in the macaque brain. This neural specialisation may have had an adaptive value for primates. This is clear when discussing social learning, in particular learning new methods of food acquisition and extraction as stated in the extractive foraging hypothesis for the evolution of primate intelligence or for learning to use tools (Fragaszy and Visalberghi 1990, Tomasello et al 1987, Call and Tomasello 1994a, Byrne and Byrne 1993, Russon 1997). Byrne and Russon (1997) have suggested that social learning and imitation work by "priming...existing brain records". The responses of neurons to the sight of individual hand actions would enter into memory and be used in later analyses to interpret sequences of complex actions, such as used by gorillas when stripping and preparing nettles for feeding (Byrne and Byrne 1993), orangutans removing the nutrious pith from bark (Russon 1997), or vervet monkey's many methods used for gathering and processing foods (Harrison 1996).

There is evidence that some cells in premotor cortex (cortical area F5, Jeannerod et al 1995) may function in the type of visuomotor transformations which form the basis of imitation. Cells in premotor cortex (F5) fire when a monkey makes a reaching or grasping movement, or manipulates an object (Rizzolatti et al 1990). Some of these cells

with motor responses also respond to the sight of an experimenter performing the same actions which were performed by the monkey. For example, cells responded to the monkey picking up an object and the sight of an experimenter picking up the same object (di Pelligrino et al 1992, Gallese et al 1996, Rizzolatti et al 1996a). The motor neurons were probably not responding to the sight of the monkey's own arm moving towards an object and performing the action, as the motor response was also present when the action was made in the dark. The motor responses were present in the light and the dark, therefore coding the motor rather than the visual component of the action. The actions seen and performed by the monkey were usually highly specific, e.g. only responsive to precision grips. Moreover, most required the presence of an object (similar to the neurons described by Perrett et al (1989a, b). The neurons also responded when a monkey actor performed the actions.

It seems reasonable to suggest that imitation in its simplest form is reliant on a visuomotor transformation. The visual program of an action is encoded into memory (possibly in the parahippocampal gyrus, hippocampus or amygdala) and the resultant representation of the action is mapped onto neurons in premotor cortex for the action to be performed. Complex imitation as discussed earlier requires a number of visuomotor transformations to be linked together in a complex sequence. The cells studied by Rizzolatti, therefore, do not completely satisfy the requirements as a basis for imitation, but combinations (or ensembles) of similar neurons may be utilised in imitative behaviour.

The exact nature of the action combinations would be dependent on the actual actions to be imitated, which may be sequential or parallel, and may also be dependent on the complexity of the actions. Tanji and Shima (1994) trained macaques to perform sequences of three actions (push, pull or turn a handle) in a particular order. The monkeys were successful in combining separate actions into more complicated sequences of 3 actions. Recording from neurons within the supplementary motor area (SMA) of the frontal cortex, Tanji and Shima found neurons whose activity was related to the particular sequence of actions previously learnt by the monkeys. The cells were maximally active before a particular sequence of actions (e.g. push-turn-pull), but not other sequences of actions (e.g. pull-push-turn). Tanji and Shima suggested that the

neurons "seem to signal a specific order of forthcoming multiple movements to be performed on the basis of memory" (p. 413). Monkeys can, therefore learn to perform complex sequences of actions (as required for imitation), however, monkeys may not be able to copy the observed sequence of actions of other monkeys. The SMA is connected to the amygdala (see Chapter III), so visual information (coding for the sight of actions) may pass from the STS via the amygdala to the SMA (direct projections from the anterior STS to the SMA have not been reported).

7.1.3 Aims and Predictions

It is the aim of this chapter to evaluate the responses of neurons within the macaque STS and to provide an interpretation of the cells' possible function in perception of social signals. Previous studies have found that cells within the STS respond to complex visual (static and motion) stimuli (see earlier). The stimuli used in the protocols (experiments) described in this chapter, used to elicit cell responses were of human heads and bodies (static or in motion). The following sections describe the predictions/hypotheses for different cell types which may be responsive to some aspect of another's attention, (see also Perrett et al 1992).

1. Static stimuli

(a) Gaze direction

Perrett et al (1985b, 1991, 1992) reported that a large percentage of cells within the STS which were responsive to a specific view of the head were also selective for a particular direction of eye gaze. Cells sensitive to eye direction were either responsive to gaze which was compatible with the head view (e.g. eyes left, head left) or gaze direction independent to the direction of the head (e.g. eyes left, head facing or eyes left, head left). Chapter IX discusses behavioural evidence that the eyes are important predictors of another's attention. The first prediction for neurons responsive to gaze is that the maximal responses will be dependent on the direction of gaze, but independent of head view. If head and gaze direction are incompatible, the cell response would be dependent

on the direction of gaze alone. A second prediction would be that a second population of neurons may respond to either eye contact or gaze averted (as eye contact is part of a threat and eye aversion is a subordinate gesture when presented with a threat, in rhesus monkeys). Cell responses, therefore, would relate to behavioural responses (eye direction is a better predictor of attention direction than head direction and this is reflected in cellular responses).

(b) Head view

Perrett et al (1991) also found that cells selective for one head view were more copious than cells responsive to all or multiple views of the head. The majority of cells were responsive to the sight of one "characteristic" head view (face, back of head, left and right profiles). As discussed earlier, coding for recognition of faces as a class of object may only require pooling of four types of neurons responsive to only one of the four characteristic views.

A selection of the cells responsive to one characteristic view are occasionally "broadly tuned" (i.e. they respond vigorously to one head view, but less so to other views; with response diminishing with increasing distance from the best view [+/- 60-90^0]. Pooling of four broadly tuned head view cells would be sufficient for face recognition. Cells in the STS do not just code for one of the four characteristic views. Perrett et al (1991, 1992) have suggested that one function of neurons responsive to intermediate views (e.g. half profiles) maybe coding the direction of other's attention.

Just as it has been suggested that as gaze is a more important indicator of the direction of another's attention than head view; head view may also be a better predictor of attention direction than body view (Perrett et al 1992). Wachsmuth et al (1994) reported that single neurons were either sensitive to the sight of heads presented alone (with the body occluded from sight), bodies alone (wih the head occluded from sight) or combinations of heads and bodies (in the correct locations) as whole bodies. The selectivity of the majority of these neurons was also dependent on view. In all cases, head and body view sensitivity were compatible with one another (e.g. view 90^0 head and body). Head direction may be a better indicator of attention direction than body view. It

is predicted that if the view of the head and body view are incompatible (e.g. head facing left, body facing forward), the cell would respond more to the head than the body. This prediction holds true for cells with independent tuning of the head and body (i.e. the cell responds separately to both parts, when tested in isolation). If the head is obscured, the information from the head is lost, so information from the body would be required to provide cues to attention direction.

(c) Orientation

There is no evidence of an inversion effect for monkeys viewing upside-down faces with normal configuration of features (Bruce 1982). There is an inversion effect is the facial features are jumbled (Perrett et al 1988). Ethologically, an absence of this effect might aid in recognising others when suspended from the branches of trees (for example). Wachsmuth (1995) tested the effects of rotating pictures of whole bodies (vertical orientation) on cell responses to upright bodies. (It is noted here that there are differences between orientation and view. Orientation is used here to refer to rotation in the picture plane; view refers to rotation in the horizontal plane.) The majority of cells responsive to whole bodies, had responses to a particular orientation (e.g. upright); some cells generalised across orientation in the picture plane and some were broadly tuned for orientation.

A face horizontally oriented towards the viewer is probably looking at the observer. Rotating a forward facing head would not change the direction of attention. Rotating the whole body (view 0^0) produces a slightly different result, as the position of the head changes (top to bottom of view). The head may therefore be attending to a different part of the observer's body. It is predicted that if a whole body is in profile (left or right), and possibly providing a cue to attention direction, then changing vertical orientation would have a dramatic effect on the cell's response (and the direction of attention. Upright orientations (0^0, 45^0 and 315^0) of profile or half-profile views, provide information of attention direction (e.g. view 90^0, attention to the left). Inverting the body would change the direction of attention (rotating a left facing head, 180^0, would cause the resultant head to be facing to the right).

It is predicted that rotating the head (views 0^0 or 180^0) will not have an effect on cell responses to an upright head. Rotating the whole body (views 0^0 or 180^0) may have an effect on cell responses as the direction of attention of a head/body may change with rotation. It is also predicted that the responses of cells sensitive to profile bodies (coding attention direction) will be reduced if the body is rotated in the picture plane. If the cells are not coding attention direction, then rotaing the body may have no effect on the cell responses.

(d) Elevation of head posture

The majority of previously tested STS neurons were found to be responsive to head views and/or orientations which were level on the horizontal plane (however, see Perrett et al 1985b, 1992, 1993). There are many instances in behaviour where determining the focus of another's attention on the ground or in the sky is important (for example, locating predators after hearing an alarm call, Cheney and Seyfarth 1990b). It is predicted that head elevation is important for determining another's direction of attention. Two hypotheses would substantiate this view (but requiring different levels of processing). One, elevation alone may be more important than view. Cells responsive to multiple views with the same attention direction (i.e. up) should not show differences in their response (i.e. the response to left profile up would be the same as right profile up). Two, elevation and view are equally important (one specific view and one specific elevation). For example, head elevation up and view left may be the optimal stimulus for the cell; other views and elevations would reduce the cell's response. Orientation tuning may also be a part of tuning for elevation (i.e. view 90^0, orientation 315^0 is the same as head view 90^0, elevation up).

(e) Object (goal) of attention

It is also important to locate and identify the object of another's attention (whether it is a predator, food source or potential mating partner). Human and non-human animals look at interesting things in their environment . It has been suggested that following X's gaze onto the object of X's gaze (joint attention) may be used to predict

X's intentions in relation to the object. Cells responsive to motion stimuli (walking bodies and reaching hands) have been tested for the importance of interactions with objects. Perrett et al (1989a, b) reported that a population of STS neurons selective for hand actions were maximally active when the hands were in contact with objects (or were heading interactions with objects). A second type of cell was responsive when an experimenter walked towards a specific part of the laboratory (in relation to the observing monkey).

It is predicted that certain neurons responsive to specific views of static heads would require that the head was attending to an object (within view). There are two possible positive predictions for this type of cell. A goal-centred coding approach would suggest that the view of the head would be unimportant, only that an interaction occured between the head and an object. A further hypothesis would suggest the head view *and* head-object interaction was required for the cell to respond (e.g. view 90^0 towards object, but not view 270^0 towards object).

2. Motion

(a) View

Head view is vitally important for determining another's direction of attention. Motion can also provide information about where another is attending (and what they are intending). As with static stimuli, view is also important when interpreting direction of attention from motion stimuli. Perrett et al (1985a) and Oram and Perrett (1996) looked at the responses of cells to the sight of human bodies walking. Cells in the STS were selective for the direction of travel (e.g. to the observers left, towards the observer, etc.) and to the view of the walking body (compatible or incompatible to the direction of travel, e.g. walking backwards). It is predicted that for a number of cells responsive to whole body motion, the greater responses would be found for a specific view of the head and body, independent of the direction of motion (i.e. walk towards the monkey, view 0^0 or walk away from the monkey, view 0^0; see Oram and Perrett 1996).

(b) Head versus body view

Head view provides a better indicator of attention direction than body view (see earlier). This has been stressed for cells responsive to static head and body images, but would also be important for cells selective for the sight of bodies in motion. It is predicted that changing the view of the head whilst keeping the body compatible with the direction of motion, would change the cell responses. In section (a) above, a prediction was made that body view would be a better indicator of attention direction than direction of motion. This may be tested further by testing multiple views of the head moving in one direction.

(c) Object (goal) of attention.

The effect of adding a goal (object) of attention to a specific head view, for cells responsive to static heads, was emphasised earlier. The response of a number of STS neurons was dependent on the addition of an object of attention. The evidence presented for imitation and social learning would suggest that learning about objects in the world would be difficult without establishing what object an observed individual was interacting with. One prediction would therefore be, that the response of cells selective to reaching or walking would increase when a goal object was added.

7.2 Methods

7.2.1 General methods

The general physiological methods were described in Chapter VI. Two subjects described in the general methods were recorded. Subject Esther was recorded for 6 months from January 1994 to June 1994 and subject Steve was recorded for 23 months from January 1995 to December 1996 (with 9 months break to take part in the behavioural experiment (see Chapter IX). Esther had previously been tested in neurophysiological experiments (from March 1993) and Steve is currently being tested in

neurophysiological and behavioural experiments. No anatomical data is presented for Steve because of his continued participation in experiments.

7.2.2 Stimulus preparation

Static stimuli

Neurons were tested for their responses to static real 3D "junk" objects (such as toys, tools, foods, pieces of material, boxes, etc.), real 3D biological objects (heads and bodies of the experimenters) and 2D slide representations of the same biological objects. All cells were tested for responses to the static head and body and sometimes to the eyes if found to be responsive to the head. Slide stimuli were photographed using 200 ASA ectochrome slide film. The head and body stimuli were photographed against a light grey background with the person wearing uniform dull coloured clothes. The attention to objects stimuli were also photographed onto slide film. Only the head and shoulders were photographed looking at a large object (collection of fruit in a hanging net). The head was lit so that the eyes were clearly visible, and that little or no shadows were present on the completed slides.

Static stimuli had also been previously filmed using a video camera (JVC BY-11OE) which recorded onto U-matic videotape. These stimuli had been edited using a JVC editing suite (control unit RM-88U) and transferred onto a videodisk containing motion sequences, facial expressions and eye gaze. Each frame containing a static image was recorded so that the computer could control the presentation of the stimuli during a protocol (Perrett et al 1991). The videodisk was played on a Phillips VP406 LaserVision disc drive, with the images presented through a Sony colour video projector (VPH-1041 QM) and projected onto a white projection screen (4 metres from the subject).

If the 2D slide and videodisk stimuli did not cause the cell to fire, static stimuli were also presented "live", i.e. an experimenter would follow the computer protocols.

Motion stimuli

Motive stimuli were also created using the JVC videocamera, and transferred to videodisk similarly to the static stimuli (see Oram et al 1993, Oram and Perrett 1996). The presentation of the 2D stimuli was again controlled by the computer from the start and stop frame numbers of the motion sequences. The majority of motion stimuli were presented live (3D) by the experimenters. A basic protocol testing body view and direction of motion comprised four basic views (facing the monkey, left and right profiles and away from the monkey)) and two directions (compatible and incompatible to the direction of motion). In later descriptions, facing the monkey is designated 0^0, left of the monkey is designated 90^0, right of the monkey is designated 270^0 and away from the monkey is designated 180^0. 3D stimuli were also used when certain directions of motion were not present on the videodisk or when head direction was altered when relative to the body.

Reaching and walking to specific objects (goal-directed behaviour) were also tested for a number of cells; performed live following a protocol which was rehearsed to maintain compatibility between trials, experimenters and test sessions. A food tray and stand containing the subjects' food rewards was used as the object or goal of the experimenter's attention in these tests, due to its manoeuvrability, size and probable salience to the subjects (food reward = tray).

Testing methods

Every cell with a clear continuous spontaneous activity (S/A), was tested with a variety of stimuli. The sensory modality preferred by the cell was tested using visual objects, changing light levels, auditory stimuli (such as hitting objects, jangling keys, stamping feet, etc.) and tactile stimuli (stroking or grooming the monkey). Those cells found to be visually responsive were further tested (clinically) with a number of objects including faces and bodies, and objects in motion. Protocols using static or motion stimuli were then used to further study the precise response characteristics of the visually-responsive cell being investigated (see below for details).

1. Static

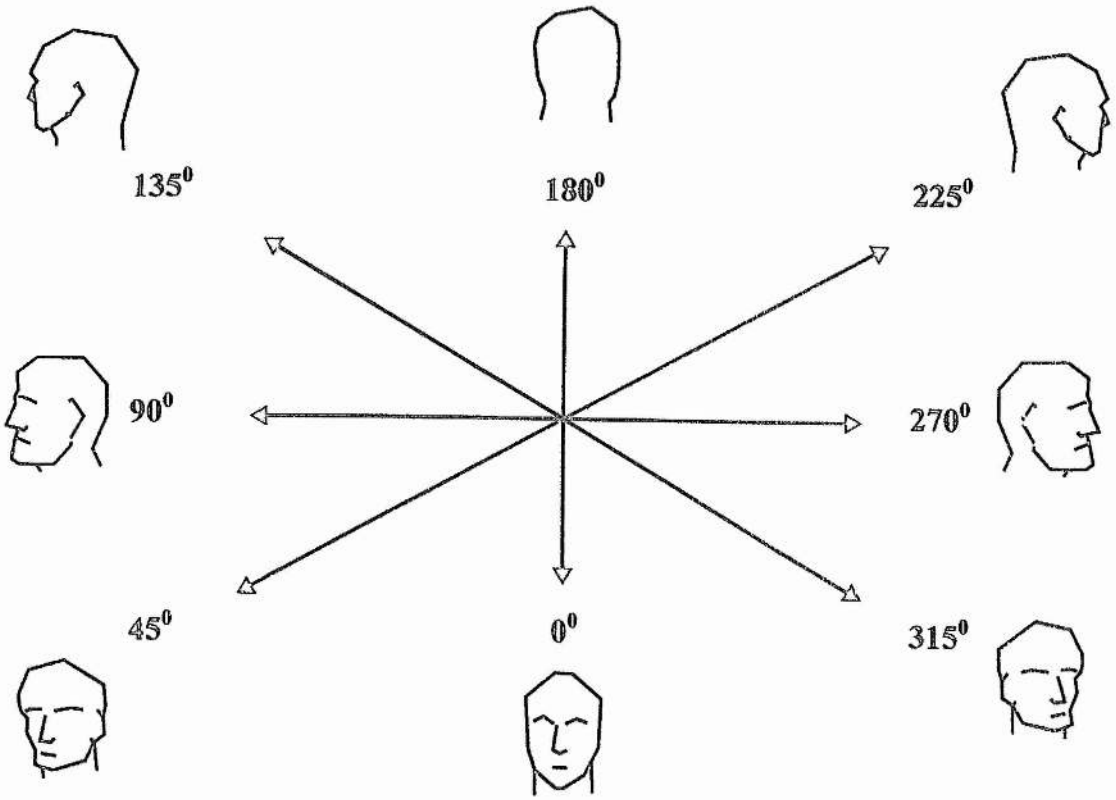
(a) Head and/or body view

A cell's response to view was tested either using live 3D stimuli (the human experiementers) or 2D images of whole bodies and heads from videodisk or slides (see earlier). For a minimum test for view; multiple views (> 2) of the same head and/or body were presented. Two views were tested for body parts (head only, body only, whole body). Four characteristic views (face, left and right profiles and back) were normally tested. For perspective view, view 0^0 corresponds to the face, view 90^0 to the left profile, view 180^0 to the back of the head/body and view 270^0 corresponds to the right profile (see Figure 7.2). Intermediate views were occasionally tested (view 45^0, 135^0, 225^0 and 315^0) with the four characteristic views. Cells which were narrowly-tuned to view had responses maximal to one view greater than other views, control objects or S/A. Cells which were broadly-tuned to view had responses to multiple views (but not all views), with responses greater than controls and S/A. Cells with object-centred coding were designated as having responses which were non-selective for view (i.e. equally responsive to all views, but greater than controls and S/A).

(b) Eye gaze

Cells selective for a specific view (only front facing and profile views) were tested for effects of changing eye position. These cells were tested using 3D heads (experimenters) or 2D head images from the videodisk. Two tests were used to determine that eye direction was more important than head view. First, the specific head view was tested with the eyes in a 1) compatible direction to the head and 2) incompatible direction to the head (approximately +/- $45\text{-}60^0$ from the head view). For example, the cell may respond to the head view 0^0. The response to the eyes would be tested at view 0^0 (compatible to the head) or view $45\text{-}60^0$ (incompatible to the head view). Second, the direction of the head was changed to determine that the initial strong response to the head may have been due to the influence of the position of the eyes. For example, the cell may respond preferentially to head view 0^0. The head view would then

Figure 7.2. Schematic representations of head view stimuli. The head was presented either on slide, videodisk or live (using one of the experimenters). Two protocols testing for the effects of head view were used, encorporating a total of either four views (0^0, 90^0, 180^0 and 270^0 from the face), or eight views (0^0, 45^0, 90^0, 135^0, 180^0, 225^0, 270^0, 315^0 from the face).



be changed (+/- 45-60^0 from preferential view), with either 1) the eyes changing to be compatible to the head (e.g. head 45^0 eyes 45^0), or 2) the direction of the eyes would remain incompatible to the head view (e.g. head 45^0, eyes 0^0).

(c) Orientation

A cell's response to orientation (rotation in the picture plane) was tested only using 2D slides of whole bodies and heads or a life-size cardboard photograph of a head (view 0^0). Eight total orientations were tested for whole bodies. Upright corresponds to 0^0, 45^0, left horizontal to 90^0, 135^0, inverted to 180^0, 225^0, right horizontal to 270^0 and 315^0. Four total orientations were tested for heads (0^0, 90^0, 180^0 and 270^0). Orientation was tested using heads and bodies with a particular view (0^0, 90^0, 180^0 or 270^0). Cells were sensitive for a particular orientation if responses were greater than other orientations, control objects and S/A.

(d) Head elevation

The effects of head elevation on the response of head selective cells were tested using 3D stimuli (the experimenters). Two tests were performed with the cells. First, the effects of head elevation, but not view on cell responses, i.e. head down, up or level (irrespective of the view; i.e. responds to view 90^0 head up and view 0^0 head up). Second, the effects of elevation and view on the cells' response, i.e. the response to head down and view 90^0 is greater than head up and view 90^0 or other view and elevation combinations, controls and S/A.

(e) Object of attention

Goal-centred coding suggests that the responses of a number of head view selective neurons are dependent on the interaction of an object with the head. Two possible tests for the effect of adding an object as a focus of the head's attention were presented to the subjects. The first protocol tested whether the response to a particular head view would be increased if an object was presented in the same visual field as a head (i.e. the head is looking towards or away from the object). This was tested by presenting

the subjects with slides of one head view (as the importance of view would have already been previously established), the same view with the head oriented towards an object (fruit hanging in a net), the same view with the head looking away from the object and the object without the head (see Figure 7.3). This protocol therefore tested, 1) whether view was important and 2) whether interacting with an object was important. A second protocol tested whether view was unimportant, but the interaction between the head and object would be important for the response of the cell (i.e. the cell always responds when the head is facing the object, independent of the head view). A minimum test for this hypothesis would be to use two head views, with views 180^0 apart. In either case, for the cell to be selective for heads interacting with objects, the response to the head and object must be greater than to the head alone, object alone and S/A. It is also predicted that the response to head looking towards the object, will be more than head looking away from the object.

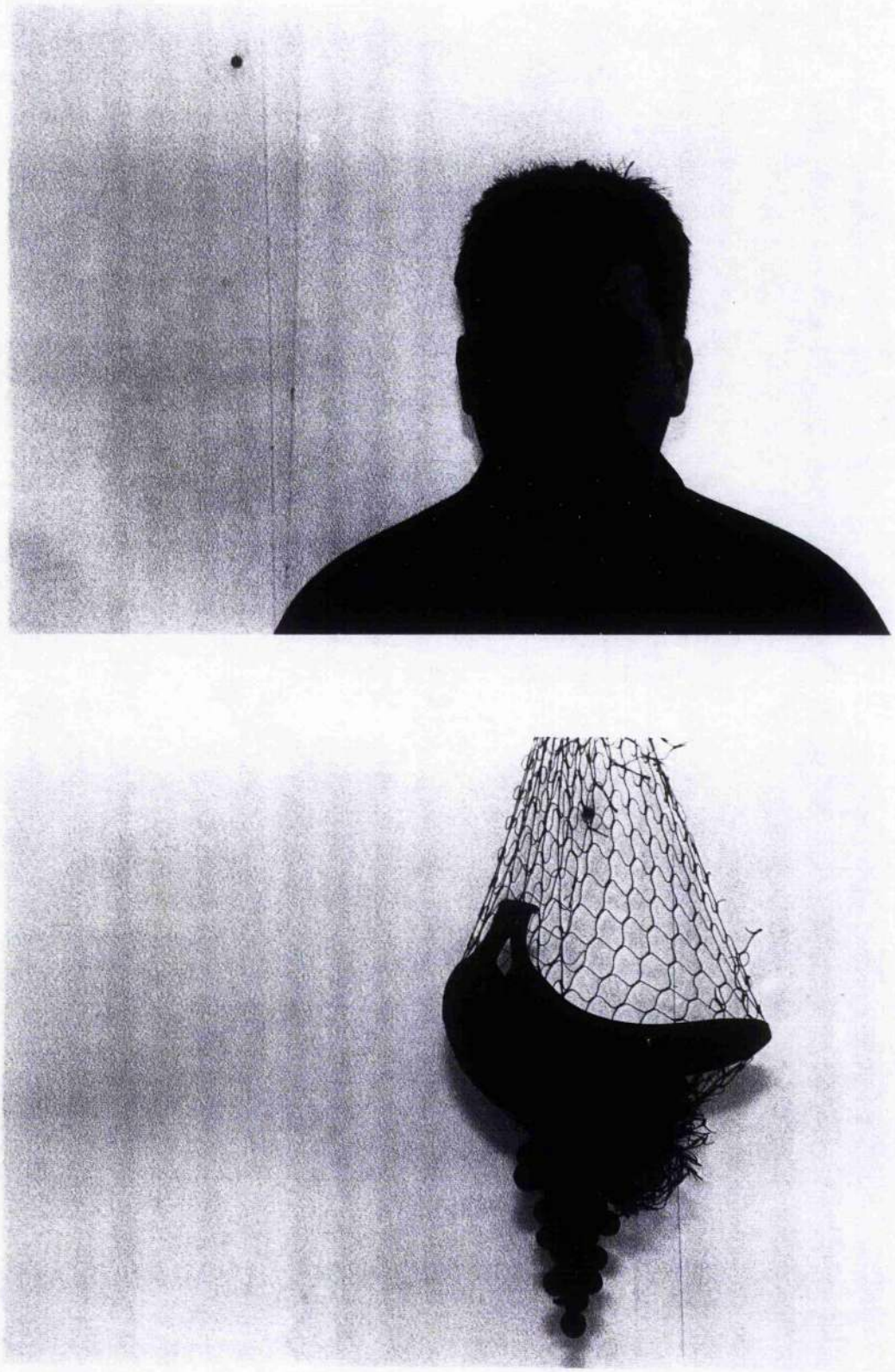
2. Motion

(a) View

View is an important indicator of another's direction of attention during movement. Cells responsive to body motion (i.e. walking) were tested for view selectivity using videodisk (see Oram and Perrett 1996) or live by experimenters. A minimum test for view sensitivity was 1) the view was compatible to the direction of motion (e.g. walk towards the monkey whilst facing the monkey) and 2) the view was incompatible to the direction of motion (e.g. walk away from the monkey whilst facing the monkey). In most circumstances, a minimum of four views were tested for compatibility with motion direction. When discussing view sensitive motion responsive cells, use of 0^0, 90^0, 180^0 and 270^0 is comparable with the use for static view responsive neurons (see Figure 7.4).

A second protocol was used to test the effect of head view and motion. The body view which caused the maximal response from the cell was tested with different head views (three in total). For example, a cell responsive to a body walking towards the monkey would be tested further with the head facing forwards, to the left or to the right. As with cells responsive to static head view, the information from the head should be

Figure 7.3. Photographic examples of slide or live stimuli used to test the effects of making an object the focus of attention of a specific head view. For a minimum protocol, four stimuli were presented to the subjects: **(a)** head view alone, **(b)** object alone, **(c)** head view looking towards an object and **(d)** head view looking away from an object.



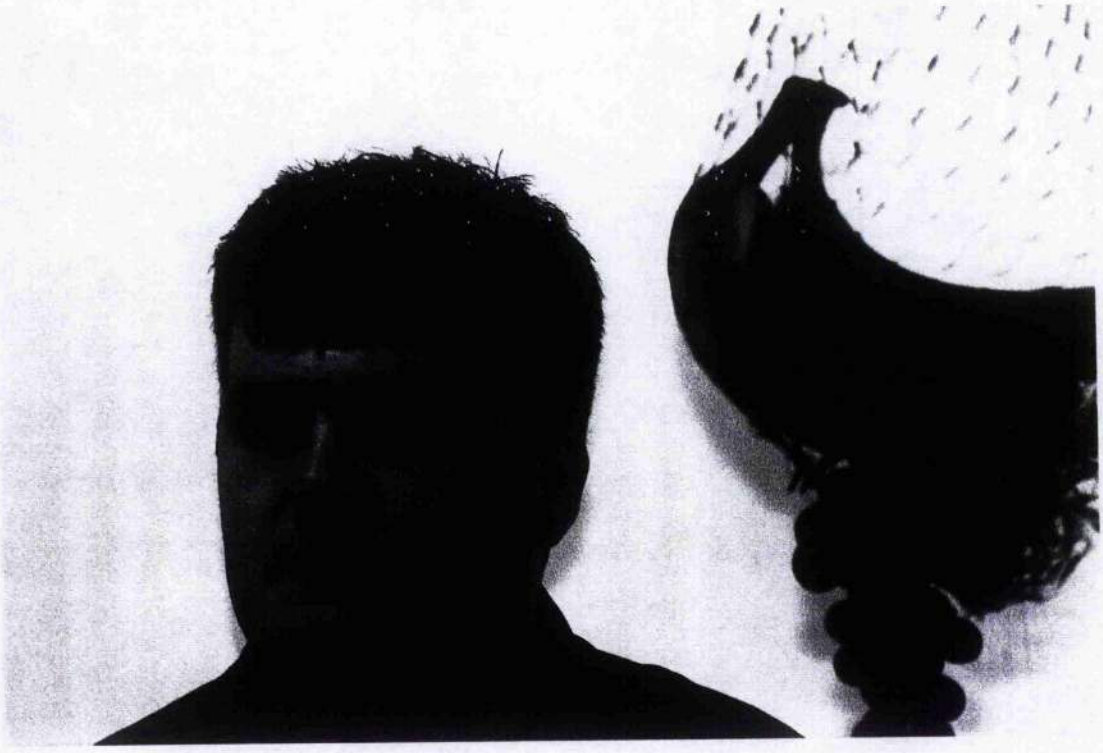
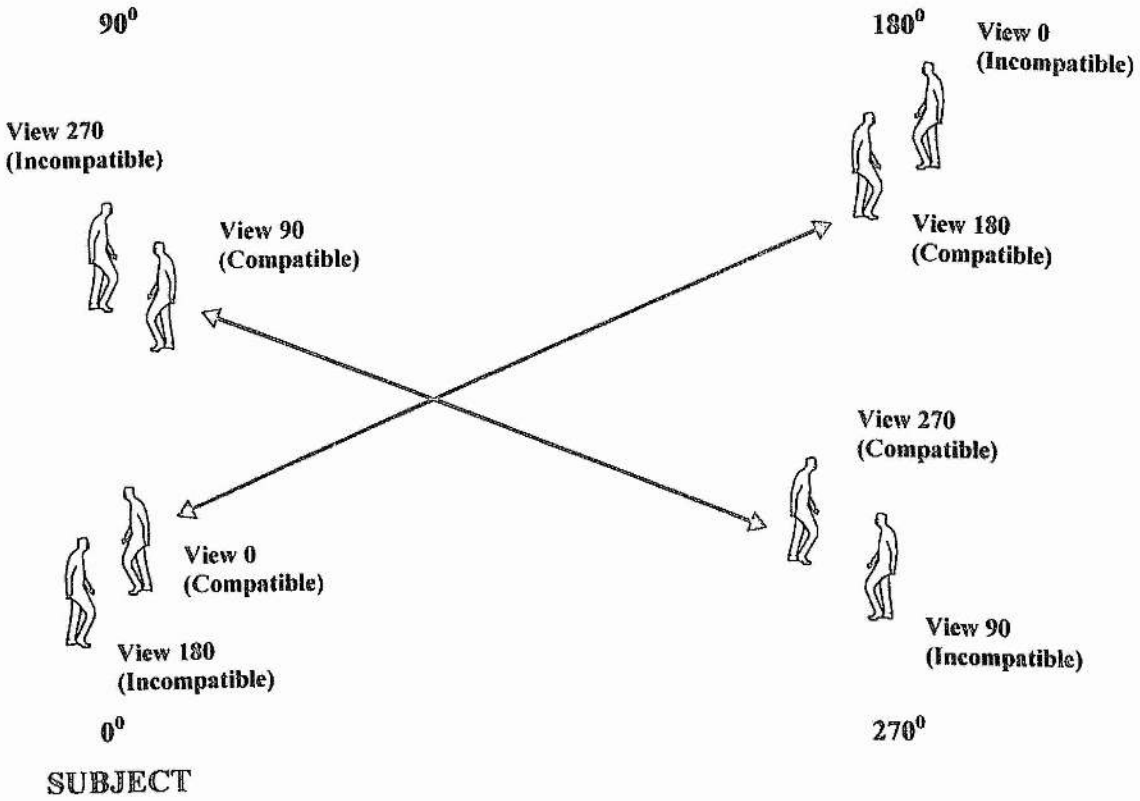


Figure 7.4. Schematic representations of motion stimuli (videodisk, videtape or live by the experimenters) used to test the effects of head and/or body view on whole body motion, and motion direction. A minimum of four views were tested (0^0, 90^0, 180^0 and 270^0 degrees from the viewer). For example, view 0 is facing the observing monkey independent on the direction of motion. A minimum of four directions were tested (go 0^0, go 90^0, go 180^0 and go 270^0). Go 0^0 was walk towards the subject, go 90^0 was walk to the left of the subject, go 180^0 was walk away from the subject and go 270^0 was walk to the right of the subject.



more important than the body for coding attention direction. The cell, therefore, should only respond to one head view, if coding for attention direction.

(b) Direction

Motion direction can potentially be used as a secondary indicator of attention direction when other cues are not available. For example, it may be difficult to analyse another's attention direction when the other individual is moving at a high speed. An eagle moving quickly towards a monkey can be assumed to be attending to the monkey, without the need to process the bird's direction of attention. The cell's response to motion direction was tested live (3D) or on videodisk (see Oram and Perrett 1996) using either one or two views and four or eight directions (towards the monkey, away from the monkey, to the left of the monkey and to the right of the monkey and intermediate direction). In discussions of cells selective for motion direction, motion towards the subject is designated "go 0^0", motion away from the subject as "go 180^0", motion to the left of the subject as "go 90^0"and motion to the left of the subject as "go 270^0" (see Figure 7.4).

(c) Object of attention

Objects or goals of attention may also increase the response of cells selective to body and/or hand motion (see Perrett et al 1989a, b, 1990b). Interactions between whole bodies in motion and objects were tested live by the experimenters. The direction of motion and specific view were previously established (cells responsive to specific view and specific direction of motion, and specific view but unspecific direction of motion were tested). A minimum protocol was similar to the minimum static protocol (walk towards the object whilst facing the object, walk away from the object whilst facing away from the object, walk towards the usual position of the object). A more complex protocol testing view and interaction with objects may include walk towards the object whilst looking away from the object, and walk away from the object whilst looking at the object. All responses to walking may be compared with responses to the object alone, the object moving away and towards a static standing body and S/A.

Data analysis

Neuronal responses to the optimum test views, directions, etc. were compared with other views, directions, etc., control objects and S/A using 1-, 2- and 3-way ANOVAs and protected least significant difference (PLSD, Snedecor and Cochran 1980, Oram 1996) *post-hoc* tests. Cells were deemed to be selective if they responded to one or more of the stimuli presented with responses significantly different from S/A. Cells may have responded as well to controls in some cases where direction of motion was more important than form. The results of the analyses were plotted as histograms of mean neuronal response (spikes per second), with SEMs. .

7.3 Results & Discussion

A total of 829 cells were recorded and isolated from three hemispheres of two monkeys. A total of 283 cells (34.1%) were recorded in Esther and a total of 546 cells (65.9%) were recorded in Steve. Cell data was collected from a total of 111 electrode penetrations (45 {40.5%}in Esther and 66 {59.5%}in Steve). Of these 829 cells, 194 cells (23.4%) were visual, 42 cells (5.1%) were auditory, 11 cells (1.3%) were tactile, 525 cells (63.3%) were unclassifiable, 16 were complex spiking cells (1.9%) and 41 were fibres (4.9%).

Of the 194 visually responsive cells, 58 (29.9%) cells were classified as visual general, or not responsive to any specific stimulus in the collection of test stimuli. Of the remaining visually responsive cells, 69 (35.6%) were classified as motion general, or responding to any stimulus moving in any direction (during clinical testing). These cells were not tested further with any of the test stimuli. Two visually responsive cells (1%) were classified as habituating to the presence of visual stimuli. In these cells, the response was high to the first presentation of the stimulus, but this response was significantly lowered on subsequent presentations. The response was recovered by the presentation of a new stimulus. Finally, 65 (33.5%) visually responsive cells were classified as having

specific responses to at least one item in the test array; species or attention/intention {static or motion}). The cells tested for responses to animal species, monkey body parts and monkey eye gaze will be described below. The cells tested for responses to human head and body views, eye gaze, attention to objects, whole body motion and motion towards objects are described in Chapter VIII.

7.3.1 General cell response characteristics

The cells recorded in the superior temporal sulcus (anterior superior temporal polysensory area) have general response characteristics. Average response (excitatory cells) to the most effective stimulus in a test array was 33.63 spikes/sec (range 0.8-104 spikes/sec, number of cells = 95) compared to an average spontaneous activity (baseline) rate of 6.8 spikes/sec (range 0-26.4 spikes/sec, number of cells = 95).

7.3.2 Specific Cell Responses

The cells types described in the following sections were extremely diverse. For this reason, and to aid in relating patterns of responses with patterns of behaviour, the results and discussion for each category of cells are combined.

1. Static stimuli

A total of 31 (out of 56 tested) cells (55.4%) were responsive to either static stimuli which may function in coding another's attention direction (eye gaze, head view or body view) or static stimuli which may require an interaction with an object.

a) Cells generalising across view (object-centred cells)

No cell which was tested for view was determined to generalise for all views presented. This finding corresponds to previous studies that only a low number of cells in the STS generalise response across all views (Perrett et al 1991, 1992). Hasselmo et al

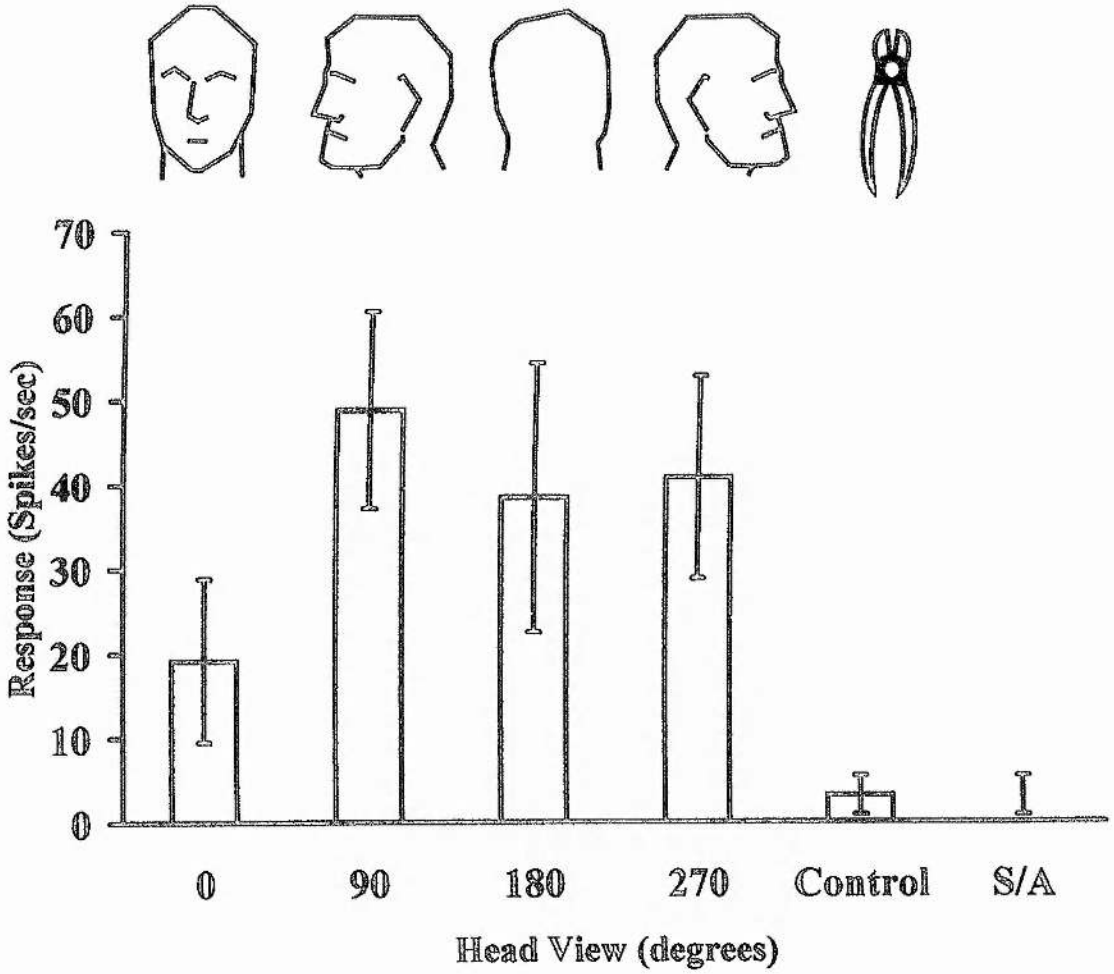
(1989) suggested that object-centred head-selective cells were abundant in the STS, however these authors did not test all views (or at least a minimum of four views were tested). The cells reported in Perrett et al (1985b) and Hasselmo et al (1989) were not tested for responses to the rear view (180^0). Moreover, cells were treated as object-centred, even when view was found to interact with identity. Perrett et al (1985b) also stated that many cells tested for view had object-centred properties, but in early studies only two views were tested.

b) Cells broadly tuned for view

Twelve cells (38.7%) were not selective to one view of the head, but were sensitive to more than one view. These cells were broadly tuned to one view, whilst remaining responsive to a number of other views, or were responsive to three views, but not to a fourth view (e.g. the face and both profiles, but not the back of the head). An example of the response of a neuron, broadly tuned to multiple views is displayed in Figure 7.5.

Cells broadly tuned to one or more views have been suggested to code for the recognition of heads and bodies. Pooling the responses of four populations of cells, each broadly tuned to one view would be required to recognise an object from any view. Broadly tuned neurons which are responsive to multiple views (not responsive to one view) may also function in coding attention direction. For example, a cell may be responsive to head view 0^0, 90^0 and 270^0, but not head view 180^0. This cell is therefore sensitive to all views of the head except the back of the head. Features of head views, 0^0, 90^0 and 270^0 are the presence of at least one ear, one eye, a nose and a certain amount of hair. The responses of these neurons may, therefore be coding for faces which are oriented towards the viewer (to a certain degree). An opposite example would be a cell which responds to head view 90^0, 180^0 and 270^0, but not to the face (head view 0^0). This neuron may be responding to all views away from the viewer (to a certain degree).

Figure 7.5. Neuronal responses of a cell broadly tuned to head view (sensitive for multiple views). Mean responses (+/- SEM, n=5 each category) to different views of the head (0^0, 90^0, 180^0 and 270^0), controls and S/A, for one cell (S32_2531). There was a significant effect of condition, ANOVA: $F(5,24)=4.28$, $p<0.01$. Three views (head view 90^0, 180^0, 270^0) were significantly different from view 0^0, controls and S/A (PLSD, $p<0.05$, all comparisons).



c) Cells specialising for one specific view (attention specific)

1. View.

Eighteen cells (58.1%) showed narrow tuning to view (i.e. a selective responsive to one specific view of the head and/or whole body). The responses to specific views displayed for these cells were significantly different from controls and S/A, and all other views tested. An example of a cell selective for view (viewer-centred) is displayed in Figure 7.6.

Three cells were responsive to the specific view of the head independent of the body view. For one cell (E99_4016), there was an effect of testing condition ($F(7,32)=7.9$, $p<0.0001$). The response to the sight of the head only (view 0^0) was not different from the whole body (view 0^0, PLSD, $p=0.89$). The responses to the head only and whole body were significantly different from the body only (view 0^0, PLSD, $p<0.0001$). The cell was also tested for multiple views of the whole body and there was a significant effect of condition ($F(5,24)=10.8$, $p<0.0001$). The response to view 0^0 was significantly greater than other views (PLSD, $p<0.05$, all comparisons). When the same cell was tested for different head views whilst keeping the body view constant (view 0^0), there was an effect of condition ($F(4,20)=9.4$, $p<0.0001$) and a greater response to head view 0^0 body view 0^0, than to head view 90^0 body view 0^0 and head view 270^0 body view 0^0 (PLSD, $p<0.05$, all comparisons).

The response of a second cell (E103_3995) was sensitive to the view of the head. A third cell was responsive only when the head was attached to the body and the views of the head and body were incongruent (see Figure 7.7). Previous studies of cells responsive to bodies and body parts (Wachsmuth et al 1994, Wachsmuth 1995) concluded that if a cell was sensitive to the appearance of both the head and the rest of the body, then sensitivity to the view of the head and body was compatible (i.e. head view 0^0, body view 0^0). The cell reported in this section was most responsive when the view of the head and body was incompatible. Behaviourally, this type of cell may be coding another's direction of attention, from head view, but while the observed animal was doing something else. (Note that the cell was only tested with static stimuli, but the response to a static stimulus may be part of coding a 'freeze-frame' of an action or

Figure 7.6. Neuronal responses of a cell selective to one view of the head (viewer-centered). Mean responses (+/- SEM, n=5 each category) to different views of the head (0^0, 90^0, 180^0, 270^0), controls and S/A for one cell (E94_3790). There was a significant effect of condition, ANOVA: $F(5,24)=13.86$), $p<0.0001$. The responses were narrowly tuned to view 180^0 and were significantly different from all other views, controls and S/A (PLSD, $p<0.01$ all comparisons). There was no evidence of backround activity (S/A).

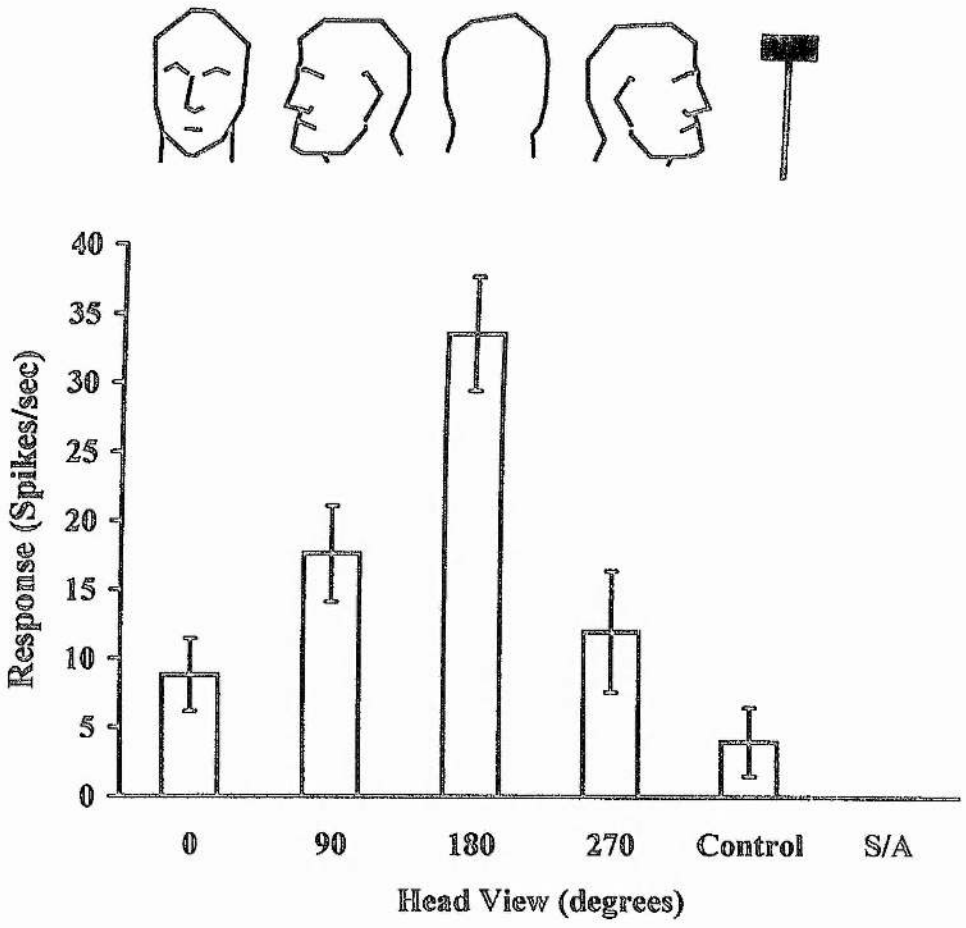
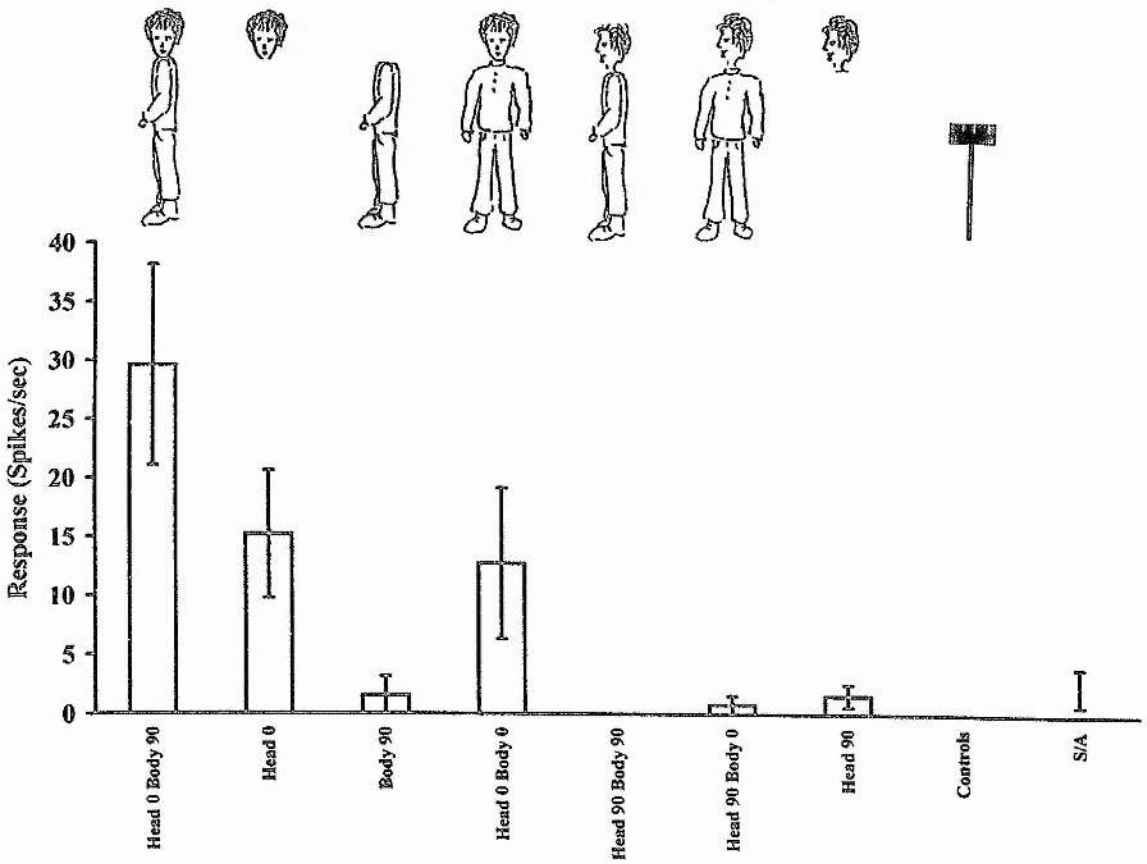


Figure 7.7. Neuronal responses of a cell selective for head and body when the views were incompatible. Mean responses (+/- SEM, n=5 each category) to different views of the head and body (separate and attached), controls and S/A for one cell (E104_3995). There was a significant effect of condition, ANOVA: $F(9,40)=6.41$, $p<0.0001$. The responses to head view 0^0, body view 90^0 were significantly different from the responses to all other stimuli, controls and S/A (PLSD, $p<0.05$, all comparisons).



motion sequence.) Vigilant animals perform actions, such as feeding, mating, etc. whilst maintaining attention elsewhere (Whiten and Byrne 1988a, Lazarus 1990). Interpreting the head view (attention direction) and body view (attention of action) may be important for social learning and predator avoidance. Another possible behavioural interpretation may be that the observed individual was studied when the individual's attention was distracted or looking over their shoulder. The body may have been directed towards one view, but a stimulus to the right of the body caused the head to move towards the right. The cell response may also be interpreted as a "follow-me" signal (see earlier), where the body is oriented in one direction, but the head is directed towards a third party.

2. Orientation.

The majority of the view specific cells described above were responsive when the head/body was presented upright. Two view (not view 0^0) specific cells (11.1%) were tested for their response to different vertical orientations (upright, left and right horizontal, inverted) of the whole body (see Figure 7.8 for details of a cell responsive to view 90^0, which failed to respond to inverted orientations).

Both cells tested for the effects of vertical orientation were found to be responsive to upright orientations (0^0, 45^0, 315^0) significantly more than inverted and horizontal orientations. It was predicted that changing the orientation of the head or body would effect the response of a cell selective to a specific view. The prediction stated that changing the orientation would also change the view. For example, the cell described above responded to view 90^0. Inverting the body changed the view to 270^0. The cell only responded to upright orientations which would have maintained the view (90^0), and therefore the direction of attention.

A cell responsive to the face (view 0^0) was tested for the effects of changing orientation. The responses of this cell are described in Figure 7.9. It was predicted that orienting a face would not change the face's attention direction (towards the viewer). There was no effect of changing the orientation of the face on the responses of this cell. The responses of the cell may be generalising across orientation. Orienting the whole body may have affected attention direction, as the head would be placed into a different

Figure 7.8. Neuronal responses of a cell selective to one view of the body (view 90^0) in an upright vertical orientation. Mean responses (+/- SEM, n=5 each category) to different orientations of the body (view 90^0), controls and S/A for one cell (E86_3843). Previous testing determined that the cell was responsive to view 90^0. There was a significant effect of condition, ANOVA: $F(9,40)=5.27$, $p<0.0001$. The cell was tested for responses to 8 orientations of the body (0^0, 45^0, 90^0, 135^0, 180^0, 225^0, 270^0 and 315^0 from upright) and there were no significant differences between the upright orientations (0^0, 45^0 and 315^0; PLSD, $p>0.05$ all comparisons), but there were significant differences between the upright orientations and other orientations (90^0, 135^0, 180^0, 225^0 and 270^0), controls and S/A (PLSD, $p<0.05$ all comparisons).

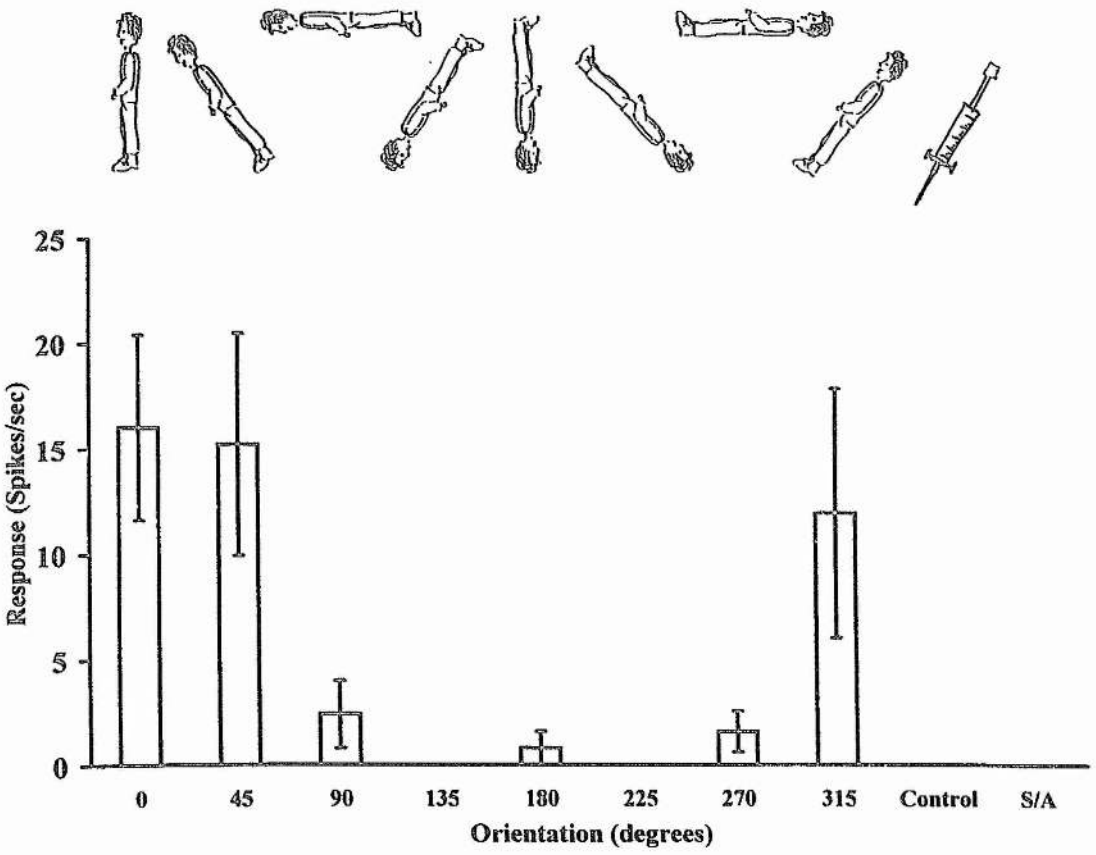
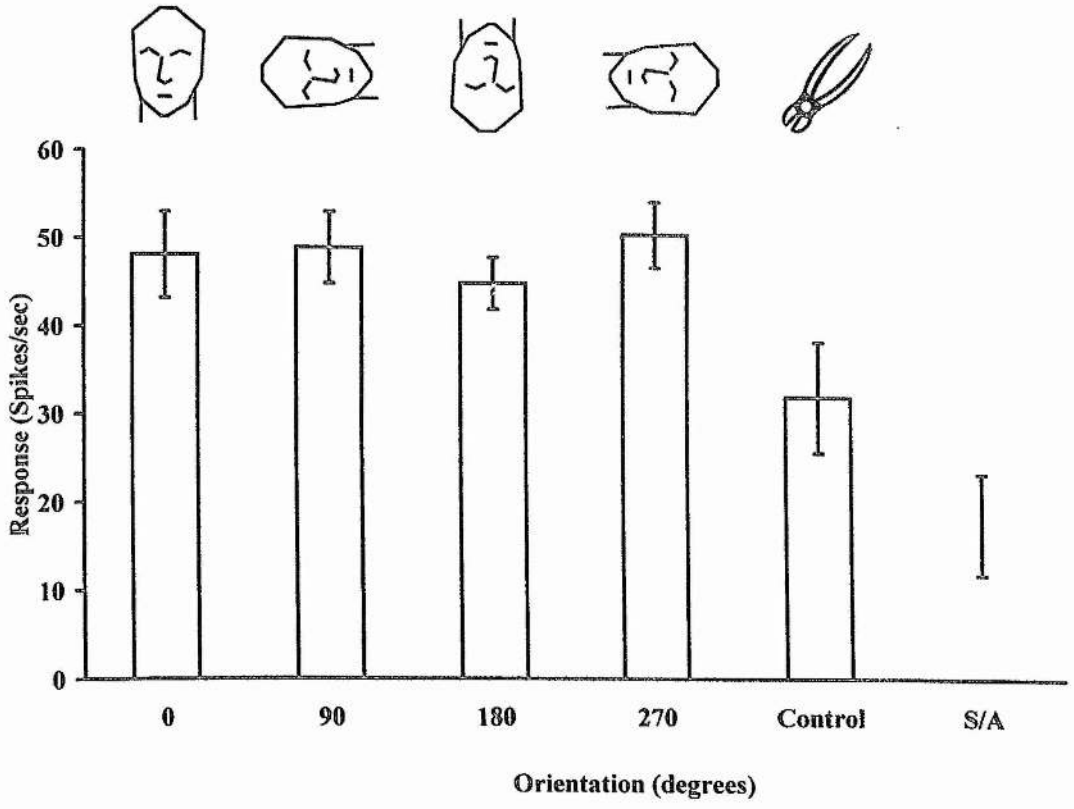


Figure 7.9. Neuronal responses of a cell generalising across multiple vertical orientations of the face (horizontal head view 0^0). Mean responses (+/- SEM, n=5 each category) to four vertical orientations (0^0, 90^0, 180^0, 270^0) of the face (view 0^0), controls and S/A for one cell (S33_2615). The stimulus was a cardboard mounted photograph of a face. There was a significant effect of condition, ANOVA: $F(5,24)=7.39$, $p<0.0001$. There were no significant differences between orientations 0^0, 90^0 and 270^0 (PLSD, $p>0.05$), but there were significant differences between orientations 0^0, 90^0 and 270^0 and controls and S/A (PLSD, $p<0.05$, all comparisons). The three upright orientations were not significantly different from orientation 180^0 (PLSD, $p>0.05$) and orientation 180^0 was not significantly different from controls (PLSD, $p>0.05$).



location (top to bottom) and may be viewing a different part of the observer's body). The responses of cells selective to the sight of the whole body (Wachsmuth 1995), which were oriented, were affected by inversion (differences from upright). All previous studies of the effects of orientation on cell responses to heads and bodies used face or the back of bodies as stimuli (Perrett, Rolls and Caan 1982, Perrett et al 1988, Tanaka et al 1991, Wachsmuth 1995), not profile views which may signify attention direction.

3. Elevation

Another aspect of attention which has been suggested for the importance to cell coding is elevation (this is related to orientation above). One cell (5.6%) was tested for the effects on cell response by differing the elevation of the head (up, level and down). The responses of this cell are displayed in Figure 7.10.

The one cell tested above was selective to elevation (head level) and head view (view 0^0). This follows from the second prediction, that cells which code for attention direction would be sensitive to elevation and view. For the one cell tested, the response to head level (view 0^0) was significantly different from head elevation down or up (view 0^0), suggesting that the head was looking directly at the viewer's face (not above the face or towards the viewers body, Perrett et al 1984).

4. Eye gaze.

The direction of the eyes are better indicators of attention direction than head view (Perrett et al 1992). For one cell, the view of the eyes and the head were required to be in compatible directions to one another (e.g. eyes left, head left, not eyes left, head facing viewer). The responses of this cell are displayed in Figure 7.11. Changing the head view, while the eyes were directed towards right (i.e. eye direction 270^0, head view 0^0) did not produce responses which were the same or higher than the response to the head and eyes with compatible views (i.e. eye direction 270^0, head view 270^0). The response to head view 0^0, eye direction 270^0 was greater than the response to head view 0^0, eye direction 0^0. This result suggests that the cell was sensitive to gaze direction independent of the head view.

Figure 7.10. Neuronal responses of a cell selective to view and elevation of the head. Mean responses (+/- SEM, n=5 each category) to 2 different views of the head (0^0 and 180^0) with different elevations (up, level and down) for one cell (S33_2615). The cell was responsive to view 0^0 and the head level, compared to other views, elevations and S/A (PLSD, $p<0.05$ all comparisons). There was a significant effect of condition, ANOVA $F(6,28)=12.64$, $p<0.0001$. There was also a significant main effect of head view, two-way ANOVA: $F(1,8)=9.29$, $p<0.05$; and a non-significant main effect of head elevation, $F(2,2)=0.94$, $p=0.517$. There was a significant interaction between head elevation and view, $F(2,16)=16.63$, $p<0.0001$.

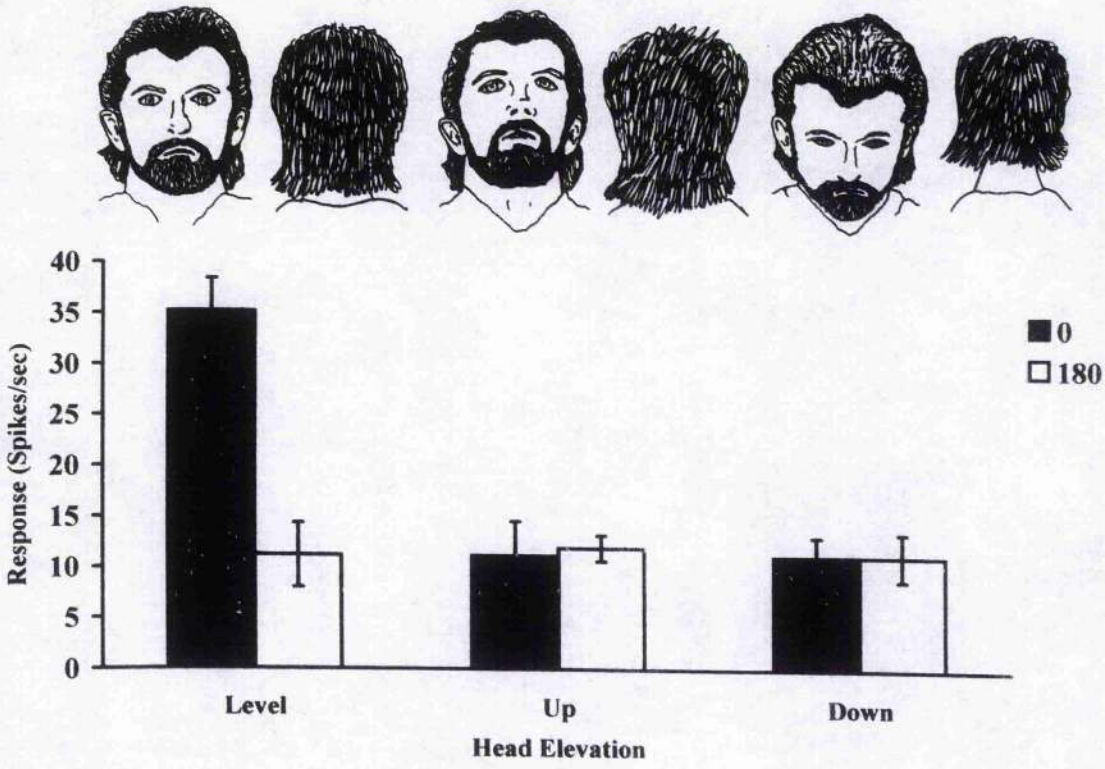
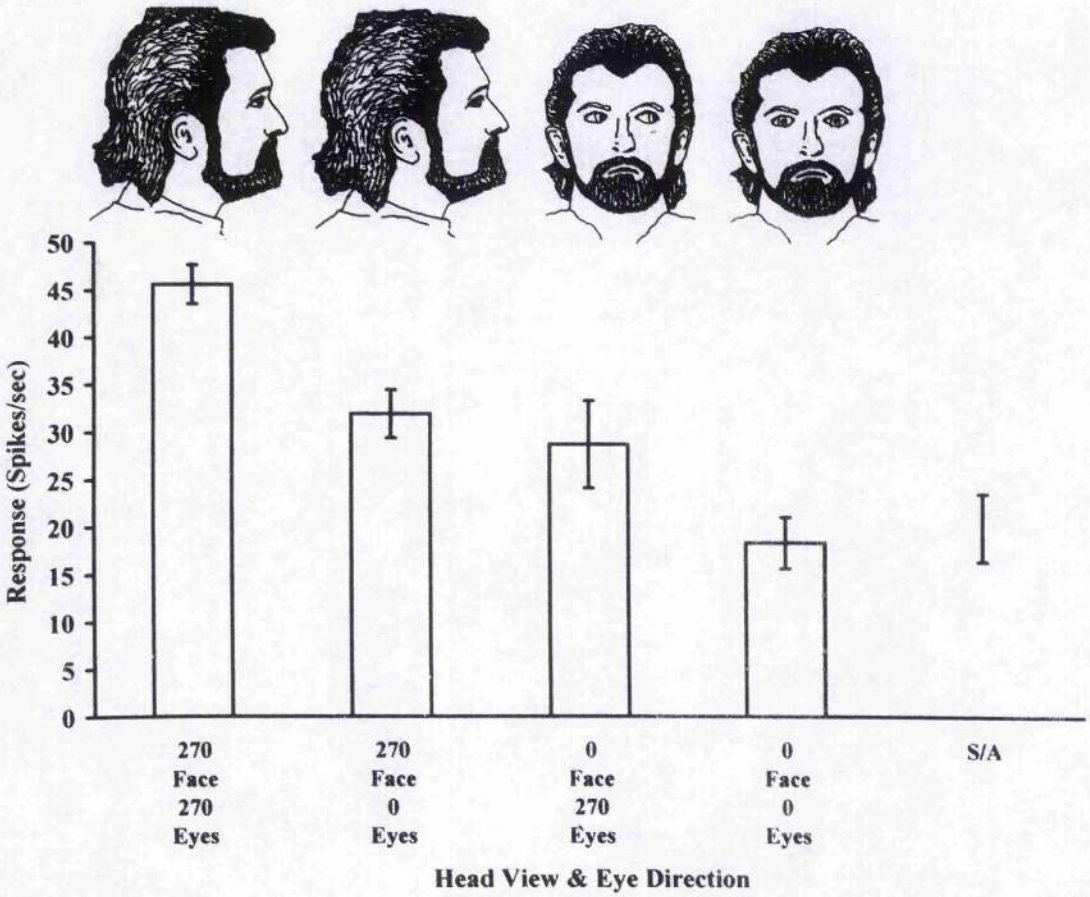


Figure 7.11. Neuronal responses of a cell selective to head view and gaze direction. Mean responses (+/- SEM, n=5 each category) to two different views of the head (0^0 and 270^0) and two different eye directions (0^0 and 270^0) for one cell (S43_2473). There was a significant effect of condition, ANOVA: $F(4,20)=11.45$, $p<0.0001$. The cell was more responsive to the head view 270^0 and eye direction 270^0 compared to other head and eye direction combinations and S/A (PLSD, $p<0.01$ all comparisons).



The responses of a second cell did not require that the eyes were directed towards a particular view, only that the eyes were present (not closed). This cell was responsive to head view, independent of eye position (see Figure 7.12). This cell appears to code the presence of the eyes on a face. One cell which was dependent on the position of the eyes was also dependent on the species of animal with the eyes (monkey not human). The responses of this cell are described in Chapter VIII.

d) Cells tested for attention to objects

Determining the direction of another's attention may be important for attributing purpose behind another's behaviour, but gaze also provides an important cue for locating objects in the environment, such as food, mating partners and predators (see chapter IX). Single or populations of neurons may respond to the sight of a head directed towards an object, but not when the head was presented alone, when the object was presented alone or when the head was looking away from the object.

Four view selective cells (22.2%) were tested for the effect on responses when an object was made the object of a human head's attention. None of the cells tested were found to responsive only to the head plus the object (looking towards or away from the object). An example of this type of response is displayed in Figure 7.13, where no differences are apperent between head alone, head towards object or head away from object.

Cells responsive to the interaction between bodies and objects were described in the introduction (Perrett et al 1989a, b, 1990b). Those cells required that the bodies were in motion and that a physical interaction (or prediction of physical interaction) occured between the body (e.g. hand) and the object. The absence of an effect of objects on static head view selective neurons may be due to the lack of a physical interaction between the heads and objects. The cells responsive to hand-object interactions described above (Perrett et al 1989a, b) required that the hands and objects were actually touching to produce a response. Only looking at an object may not be sufficient to drive the cell responses.

Figure 7.12. Neuronal responses of a cell sensitive to head view, but independent of eye position. Mean responses (+/- SEM, n=5 each category) to one view of the head (view 0^0), with eye direction, 0^0, 45^0, 315^0 or eyes occluded, for one cell (S33_2615). There was a significant efect of condition, ANOVA, $F(11,48)=5.5$, $p<0.0001$. The responses to head view 0^0 with different eye positions (0^0, 45^0 and 315^0) were significantly different from head view 0^0 with the eyes occluded, controls and S/A (PLSD, $p<0.05$, all comparisons).

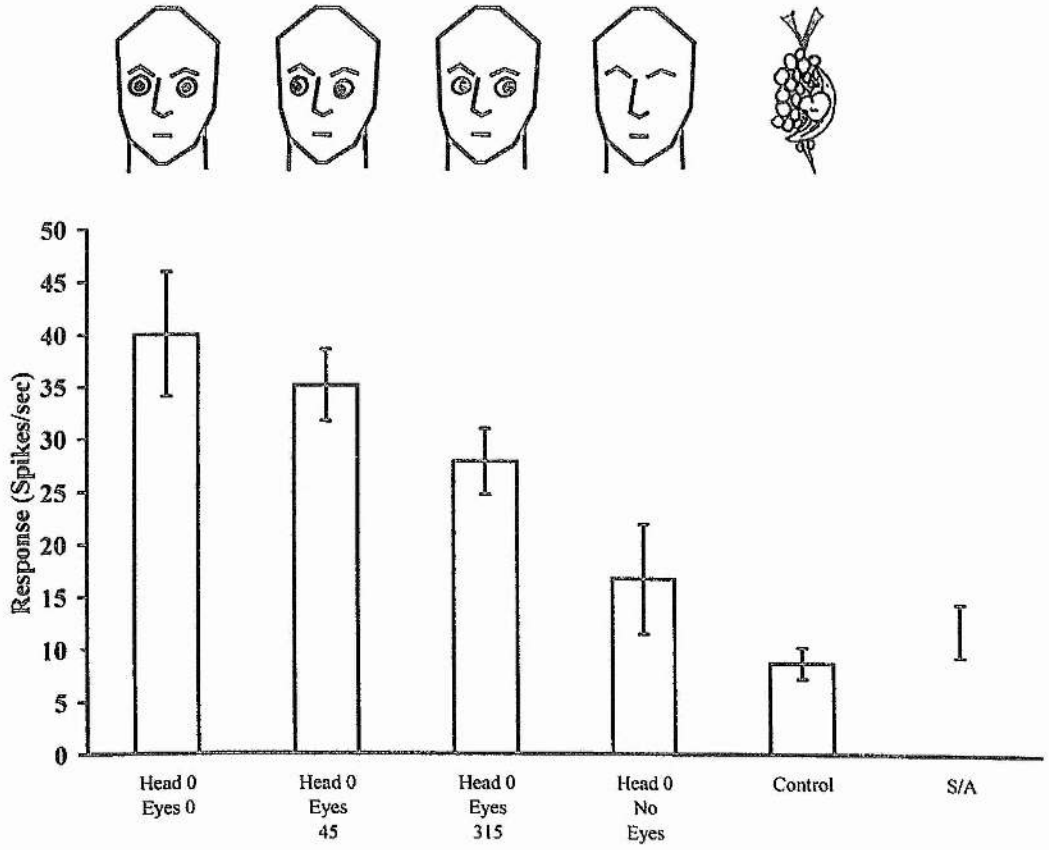
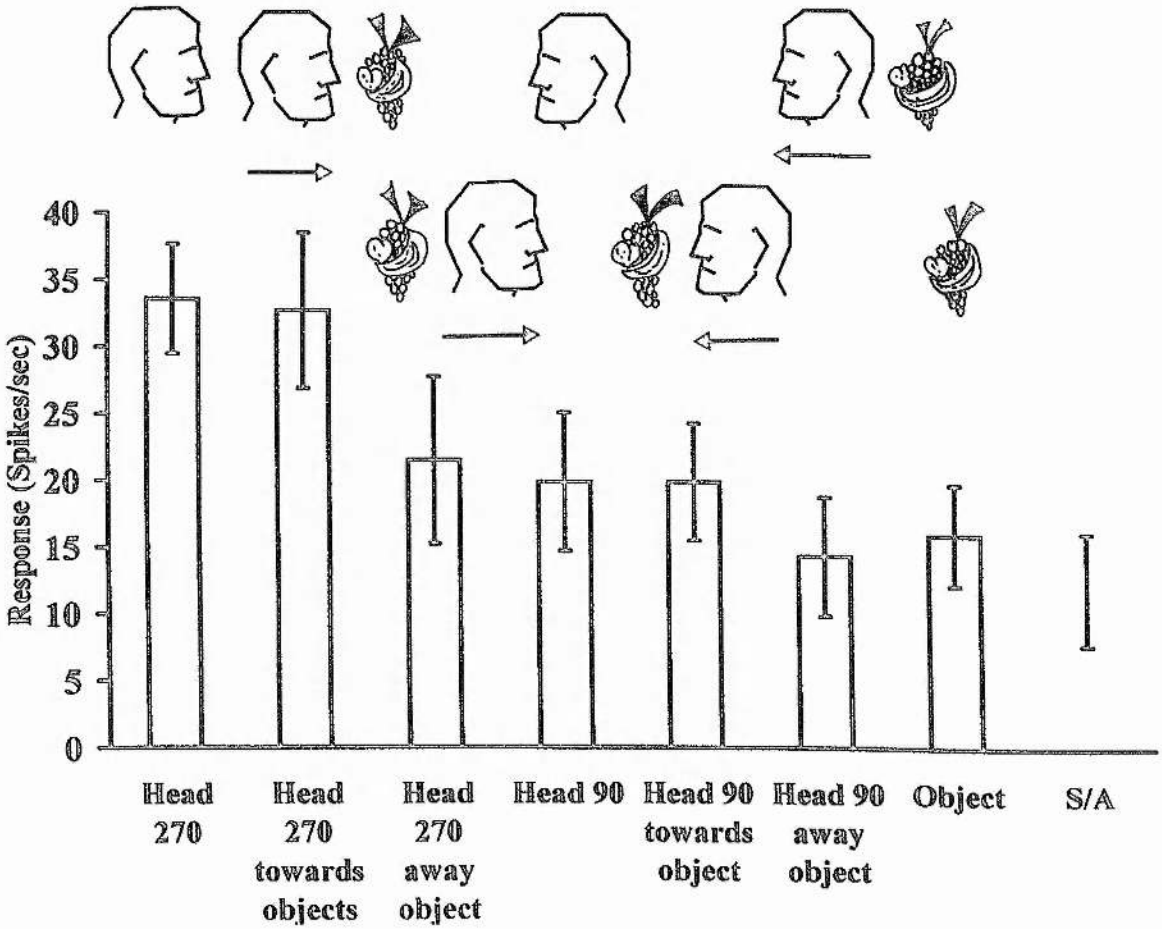


Figure 7.13. Neuronal responses of a cell responsive to head view and interaction with an object. Mean responses (+/- SEM, n=5 each category) to slides of two different views of the head (90^0 and 270^0), with the head either looking towards and away from an object (hanging collection of fruit), the head without the presence of an object, or the object without the presence of the head, for one cell (S43_2498). There was a significant effect of condition, ANOVA: $F(8,36)=3.12$, $p<0.01$. All views (in all combinations) were significantly different from S/A (PLSD, $p<0.05$). There was a significant main effect of view in a 2-way ANOVA, $F(1,8)=9.73$, $p<0.05$, but no significant effect of object presence, $F(2,2)=3.91$, $p=0.2$. There was also a non-significant interaction between view and object presence, $F(2,16)=0.21$, $p=0.81$.



Behavioural evidence in chapter IX suggests that monkeys follow another's gaze independent of the presence of an object of attention. The objects used in the slides in this study (e.g. collections of fruit) would have been salient for the subjects. All the subjects' food during a recording session was located on a stand to the right of the subject. Neurons appear to be responsive to the sight of hands reaching and bodies moving towards the usual position of the food tray (see section 7.3.2.2 e). Neurons responsive to another's direction of attention may not require that an object of attention be processed within the same receptive field. This may be of importance for two reasons. One, the object of attention may not be within the receptive field of the responsive cell (and gaze may have to be followed to some distance outside the receptive field). Second, the precise object of another's attention changes temporally, spatially and between individuals. One individual may be looking at a clump of fruit, a second may be looking at a predator, a third may be looking at a conspecific. The second individual may be looking at a predator, first by the trees, next by a pool, etc. The response profiles of neurons selective for other's heads looking at precise objects would not be flexible to code a large number of objects, spatially and temporally. The responses of the majority of neurons sensitive to hands interacting with objects (Perrett et al 1989a, b) were not dependent on the form of the object. Only the goal of the interaction was important. Determining the goal of another's behaviour may be more difficult when using information from static stimuli, such as a head looking at an object. More information concerning the intentions of the head towards the object are gained if the head moves towards the object. Static stimuli, however, appear to be sufficient stimuli for human children to interpret another's gaze within an intentional framework (Baron-Cohen 1994, 1995, Baron-Cohen et al 1995). Non-human primates may only be able to utilise motion cues to help understand another's purposive behaviour.

It is possible that a number of neurons in the temporal lobe do code for the sight of other's heads interacting with objects. The small sample of neurons described in this chapter provide evidence which is indicative, but not conclusive that such neurons are not to be found within the cortex of the STS.

2. Motion stimuli

A total of 25 (44.6%) cells were responsive to motion stimuli (heads and bodies in motion) or motion stimuli where an interaction with objects (i.e. walk to an object) elicited cell responses. A number of these cells may represent the direction of another's attention (view specificity during motion).

a) Cells sensitive to motion direction with compatible body view

All cells tested were selective for direction of motion and/or head and body view. Seven cells (28%) were non-selective for a particular view or direction of motion, but required that the view and direction of motion were compatible to one another. An example of a cell response is displayed in Figure 7.14. It is noted that this type of cell differs from motion general cells, in that these cells require coding of a specific form as well as motion to respond (such as walking bodies, not moving trolleys). All form-selective motion responsive cells described in the following sections respond preferentially to walking three-dimensional bodies or representations of 3-D bodies.

b) Cells sensitive to motion direction, but not body view

Six cells (24%) were selective for the direction of motion, but not for the view. Some of these cells were non-form selective, as they were responsive to control objects moving in the appropriate direction. An example cell is displayed in Figure 7.15. This cell appeared to be responsive to motion towards a particular location, but not specific for the form of the object moving towards that location. An ability to determine the motion of objects without discrimnating form can have a number of functions. Oram and Perrett (1996) stated that cells responsive for direction of motion only were responsive 35msec earlier than cells responsive to form and motion direction. Everyday survival of an animal may not require or allow complex form processing to occur. For example, a predator may be hidden in bushes, where only the motion of the leaves provides a cue for the direction of the predators motion.

Some of these cells were sensitive to form and responded to bodies moving in a specific motion direction, but were not selective for the view of the head on the walking

Figure 7.14. Neuronal responses of a cell sensitive to compatible motion direction and view. Mean responses (+/- SEM, n=5 each category) to four directions of walking (go 0^0, go 90^0, go 180^0 and go 270^0), two views (compatible and incompatible) and to control motion, for one cell (S48_2150). There was a significant effect of condition, ANOVA: $F(12,52)=6.03$, $p<0.0001$. A 2-way ANOVA revealed a significant main effect of motion direction: $F(3,16)=5.13$, $p<0.01$; and a significant main effect of view (compatible v incompatible), ANOVA: $F(2,6)=33.98$, $p<0.001$. There was a non-significant interaction between view and motion direction, $F(6,32)=0.64$, $p=0.7$.

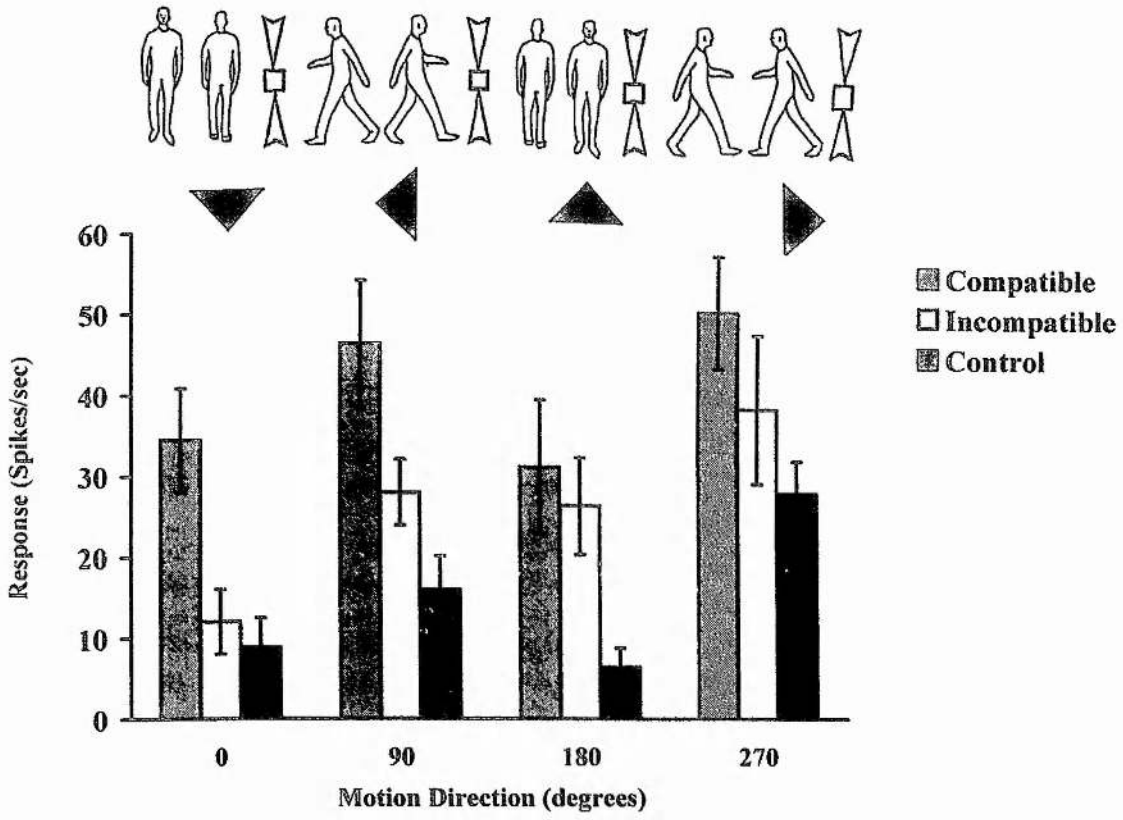
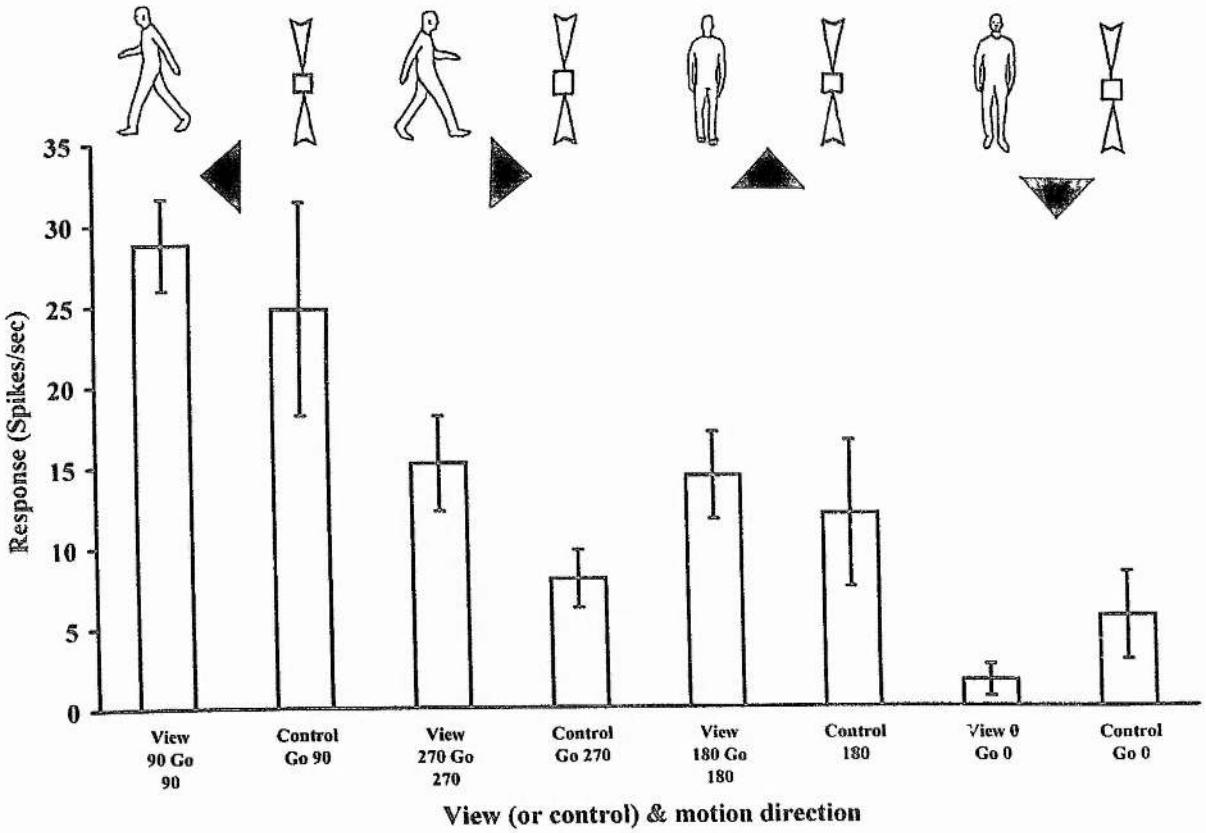


Figure 7.15. Neuronal responses of a cell sensitive to motion direction, but not form. Mean responses (+/- SEM, n=5 each category) to four directions of walking with compatible view (go 0^0, go 90^0, go 180^0 and go 270^0) and to moving controls, for one cell (S53_2669). There was a significant effect of condition, ANOVA: $F(12,52)=6.44$, $p<0.0001$. Responses to view 90^0 go 90^0 and controls moving 90^0 were significantly different from all other directions (independent of view or control, PLSD, $p<0.05$ all comparisons). There was a significant main effect of motion direction, 2-way ANOVA, $F(3,16)=12.2$, $p<0.001$; and a non-significant main effect of form (compatible view or control), $F(1,3)=0.553$, $p=0.6$. There was a non-significant interaction between motion direction and form, $F(6,16)=1.16$, $p=0.36$.



body (such as the responses of the cell displayed in Figure 7.16). This cell may be responsive to motion information from the body only, independent of head view. The cell was not tested for responses to motion of the body only.

c) Cells sensitive to body view, not motion direction

One cell (4%) was selective for the view of the body, but not the direction of motion. This cell was maximally responsive to view 0^0, than other views, controls and S/A, but did not differentiate between move towards the monkey (go 0^0) or move away from the monkey (go 180^0). The cell, therefore responded to facing the monkey, independent of the motion direction (move towards or away from the monkey). The response of this cell are shown in Figure 7.17.

This cell may be responding to attention direction cues, as the view of the head and body, not the direction of motion appear to be important. For example, responses to walking towards or away from the monkey whilst looking at the monkey, may signal interest in the monkey. Similarly, responses to attention left, independent of the direction of motion may signal interest in an object, location or event to the left.

d) Cells sensitive to motion direction and body view

Eleven cells (44%) required that walking bodies were moving in one direction with the head and body in a compatible view to the direction of motion (i.e. walking towards the monkey with the head and/or body view also directed towards the monkey). An example of this type of cell is displayed in Figure 7.18.

One cell (9.1%) was responsive to direction and view, required that the walking body went out of sight of the subject (exited) at the end of travel. The cell was maximally responsive when the body walked to the right, with the head and body pointed to the right and the body exited the monkey's visual field (see Figure 7.19).

Cells with responses to one specific direction of motion and one specific view may signal the direction of attention of the observed figure. Furthermore, the cell may also function in interpreting another's intentions in relation to objects, events or locations, at the end point of the motion. For example, an individual walking to the right

Figure 7.16. Neuronal responses of a cell selective for motion direction (go 225^0), not head view. Mean responses (+/- SEM, n=5 each category) to one direction of walking (go 225), three head views (90^0, 180^0, 270^0), controls and S/A, for one cell (E94_3818). No other directions of motion were tested. There was a significant effect of condition, ANOVA: $F(4,20)=10.24$, $p<0.0001$. Responses to all head views moving were significantly different from controls and S/A (PLSD, $p<0.05$ all comparisons).

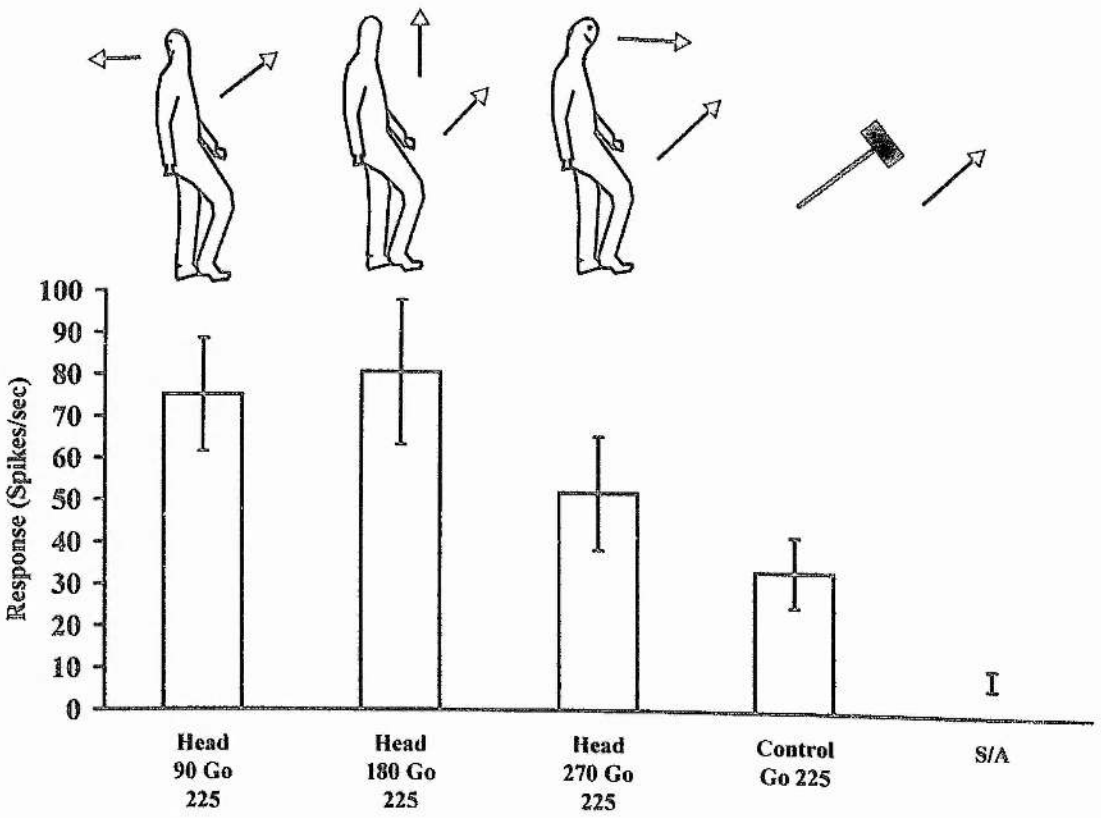


Figure 7.17. Neuronal responses of a cell selective for head/body view (0^0), not motion direction. Mean responses (+/- SEM, n=5 each category) to four directions of walking (go 0^0, go 90^0, go 180^0, go 270^0), 2 views (compatible and incompatible) and to control motion, for one cell (E95_3805). There was a significant effect of condition, ANOVA: $F(12,52)=6.62$, $p<0.0001$. Differences between head view 0^0 (go 0^0 and go 180^0) and other views and controls were significant (PLSD, $p<0.05$ or almost significant, $p=0.1$).

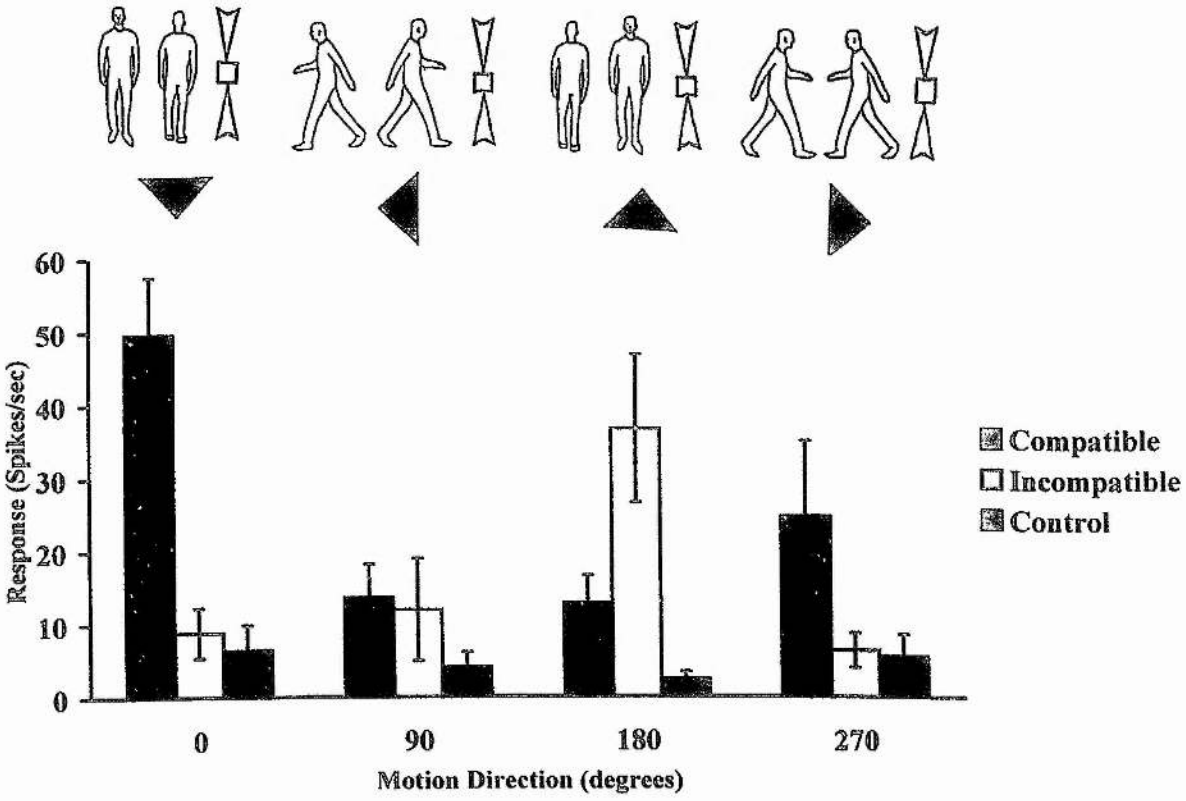


Figure 7.18. Neuronal responses of a cell selective for motion direction and head/body view. Mean response (+/- SEM, n=5 each category) to four directions of walking (go 0^0, go 90^0, go 180^0, go 270^0), two views (compatible with motion direction and incompatible with motion direction) and moving controls, for one cell (E80_3589). There was a significant effect of condition, ANOVA: $F(12,52)=5.77$, $p<0.0001$. The response to view 270^0 go 270^0 (compatible 270^0) was significantly greater than the other views, directions, controls and S/A (PLSD, $p<0.05$ all comparisons). This was confirmed in a 2-way ANOVA which revealed a non-significant main effect of motion direction, $F(3,16)=2.51$, $p=0.1$); a significant main effect of view, $F(2,6)=6.32$, $p<0.05$ and a significant interaction between motion direction and view, $F(6,32)=2.7$, $p<0.05$.

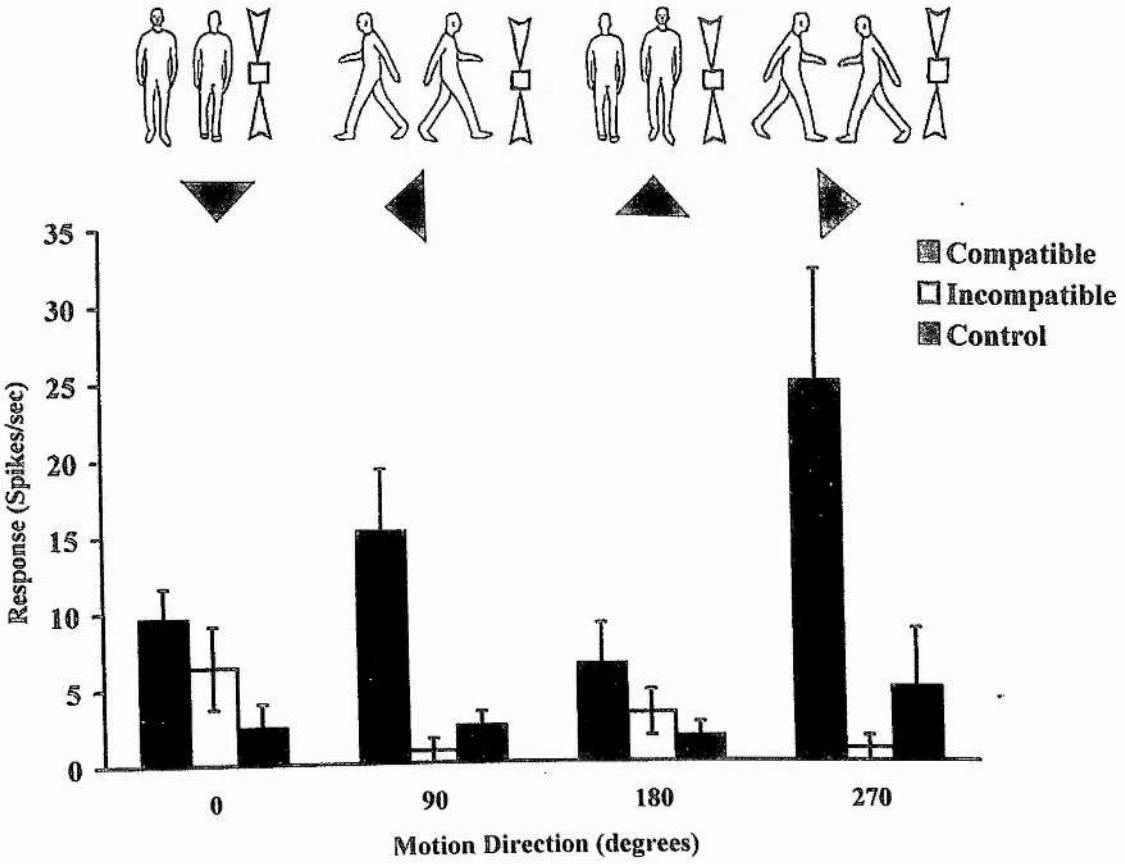
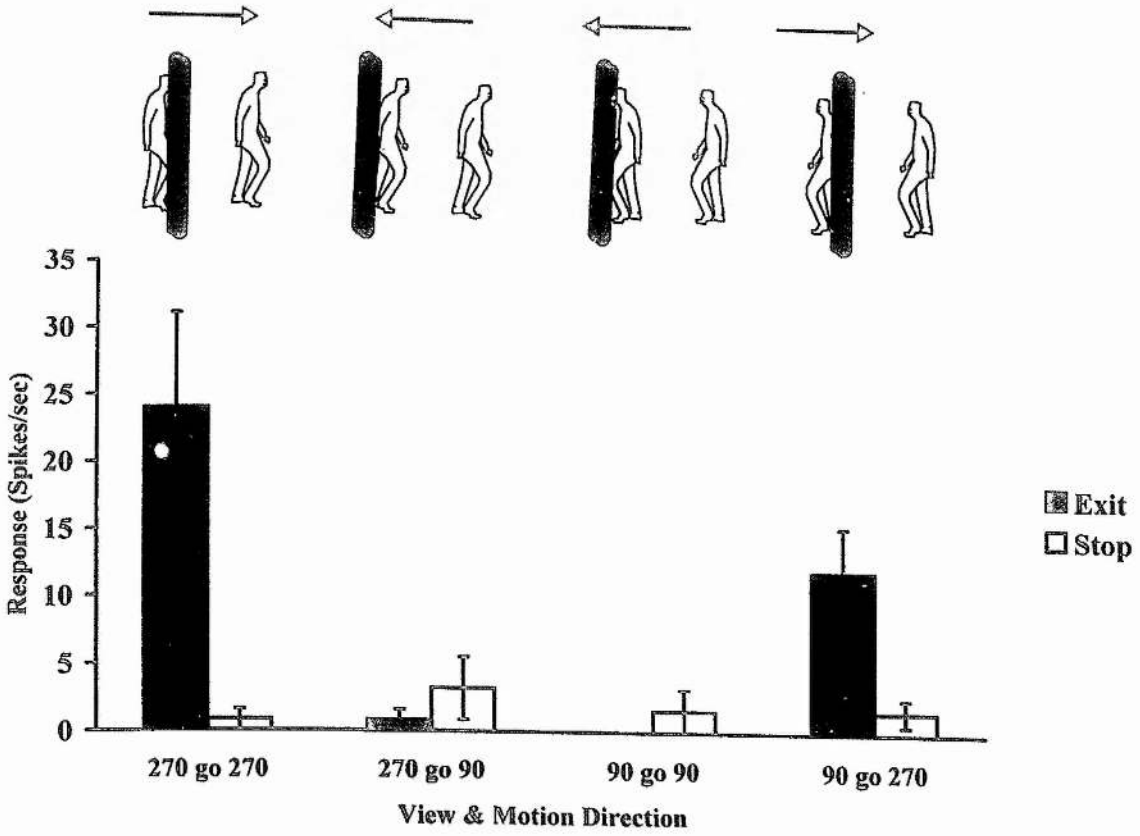


Figure 7.19. Neuronal responses of a cell sensitive to motion direction, head/body view and type of motion (exit/stop). Mean response (+/- SEM, n=5 each category) to two directions of motion (go 90^0 and go 270^0), two views (90^0 and 270^0; compatible and incompatible to the direction of motion) and type of motion (exit or stop), for one cell (S19_2166). There was a significant effect of condition, ANOVA: $F(10,44)=7.68$, $p<0.0001$. The response to view 270^0 go 270^0 exit was significantly greater than other views, exit/stop, controls and S/A (PLSD, $p<0.01$, all comparisons). The response to control go 90^0 was 2.4 spikes/sec (+/- 2.4 SEM), the response to control go 270^0 was 0.8 spikes/sec (+/- 0.8 SEM) and the S/A was 0 spikes/sec (+/- 0 SEM). The results of a 3-way ANOVA revealed a significant main effect of direction, $F(1,32)=48.3$, $p < 0.0001$; a significant main effect of view, $F(1,32)=7.7$, $p < 0.01$ and a significant main effect of motion type, $F(1,32)=42.9$, $p < 0.0001$. There was a significant 3-way interaction between motion type, direction and view, $F(1,32)=10.1$, $p < 0.01$.



with view to the right, starting at a location left of the monkey, may be interested in and intend to move towards an object, location or event to the right of the monkey. The cell with a response to a specific view and direction of motion while exiting, may also be responsive to attention direction and intention towards an occluded object or object not within the observing monkey's receptive field. The cell was not as responsive when the motion remained in view. This may signify that the end point of the motion was not within view.

e) Cells sensitive to reaching and motion to objects

The final class of cells were responsive to motion towards objects or exact locations (reaching or walking), in a goal-directed manner. Three (out of 11 tested) view and direction specific cells (27.3%), one (out of 18 tested) view specific static cells (5.6%) and two (out of 7 tested) general view and direction motion cells (28.6%) were tested for responses when an object was made the object of attention, during motion towards that object. One cell, S20_2268 (out of 7 tested) responded to reaching towards or moving the whole body towards the usual position of the food tray (which held the subject's fruit and nut rewards). The cell's response was not contingent on the appearance of the tray (or a goal object, see Figure 7.20).

A second cell (S30_2564) was responsive when the whole body walked towards the subject (go 0^0) with compatible view (view 0^0), but was also walking away from an object (a food tray on a stand), compared to walking to an object or walking without an object. A histogram displaying this cell's response is displayed in Figure 7.21.

The first cell described above responded to reaching or walking towards a particular location, but responses were not contingent on the presence of an object. Perrett et al (1989a, b) stated that the responses of the majority of the cells sensitive to actions were dependent on the presence of an object. The cell reported here corresponds to the cell reported in Perrett et al (1990b), where the response was contingent on walking to a precise location (the laboratory door). The responses of the cell described above were independent of the presence of an object, but the motion had to be directed towards the particular location, not away from it.

Figure 7.20. Neuronal responses of a cell sensitive interaction with an object (or usual location of the object). Mean response (+/- SEM, n=5 each category) to a hand reaching to or retracting from an object or whole body motion towards an object (tray present or not present), for one cell (S20_2268). There was a significant effect of condition, ANOVA: $F(6,28)=2.68$, $p < 0.05$. The responses to reach towards or move towards tray position were significantly different from move body to tray, retract hand from tray and S/A (PLSD, $p < 0.05$, all comparisons). All other comparisons were non-significant (PLSD, $p > 0.05$). A 2-way ANOVA revealed a significant main effect of presence of the tray, $F(1,8)=5.33$, $p < 0.05$ and a non-significant effect of motion type (reach, retract, move body), $F(2,2)=12.87$, $p = 0.07$. There was a non-significant interaction between presence of the tray (object) and motion type, $F(2,16)=0.28$, $p = 0.76$.

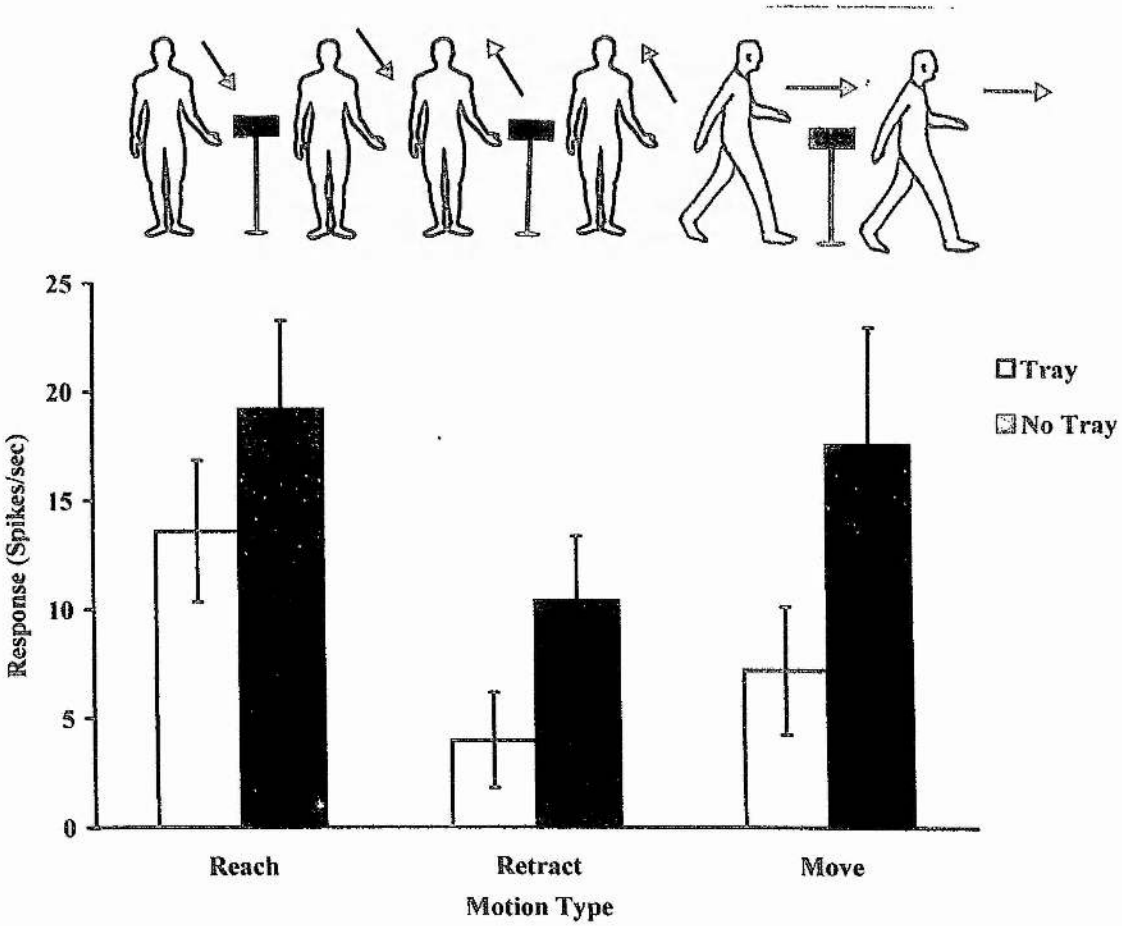
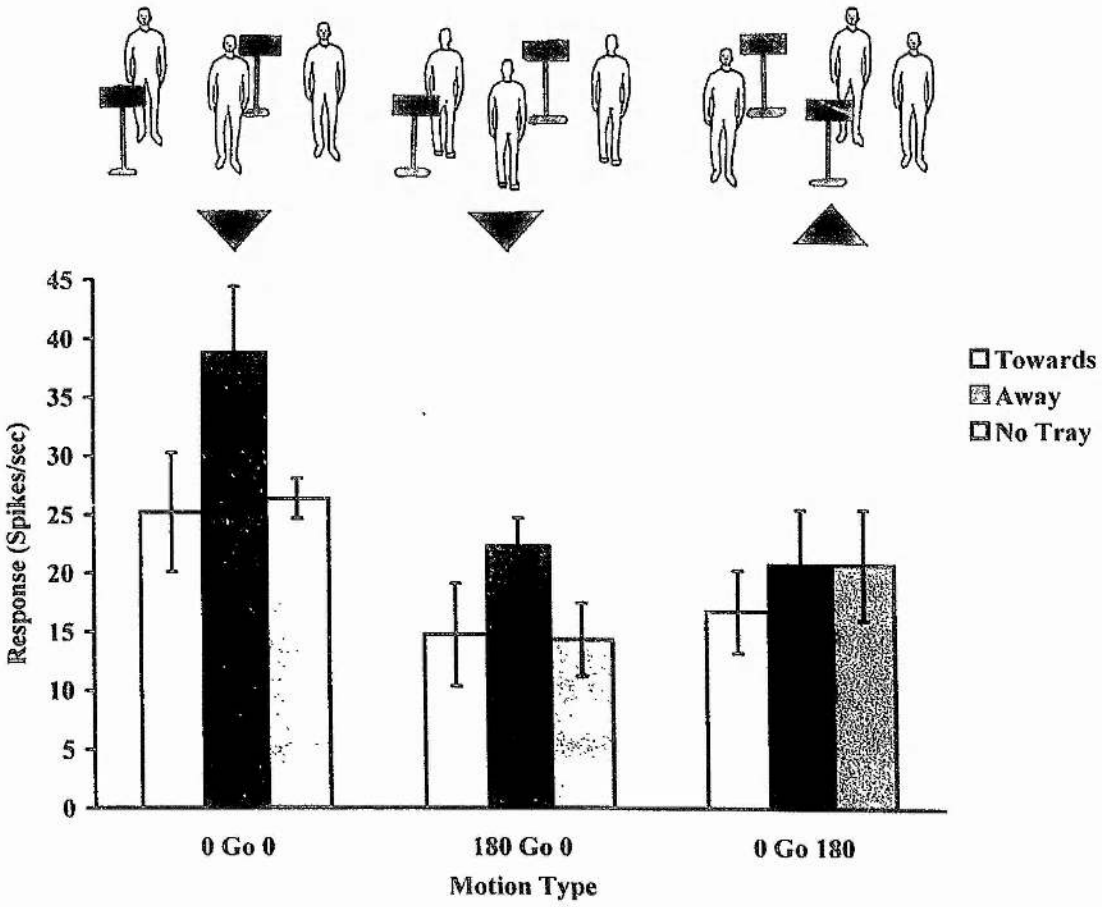


Figure 7.21. Neuronal responses of a cell sensitive to whole body motion away from an object. Mean responses (+/- SEM, n=5 each category) to a whole body walking (view 0^0 go 0^0, view 180^0 go 0^0 or view 0^0 go 180^0) towards or away from an object (a food tray) or walking (all views and directions above) to the position of the tray (tray not present), for one cell (S30_2564). There was a significant effect of condition, ANOVA: $F(9,40)=2.79$, $p < 0.01$. There were significant differences between view 0^0 go 0^0 away from the tray and all other stimuli and S/A (PLSD, $p < 0.05$, all comparisons). A 2-way ANOVA revealed a significant main effect of view and motion direction, $F(2,4)=12.63$, $p < 0.05$, a non-significant effect of motion type (walk to and away from tray and walk to tray position), ANOVA: $F(2,12)=3.07$, $p = 0.08$ and a non-significant interaction between motion type and view/motion direction, $F(4,24)=0.71$, $p = 0.59$.



The responses of the second cell were dependent on the presence of the object. The whole body motion had to be directed away from the object. The object had to be in a particular location as the view and direction of motion were also important. For example, the cell responded to walk towards the monkey while attending to the monkey and walking away from the object. This may correspond to walk to the monkey with a fruit reward (as the food tray was the object). The cell did not respond to walk towards the monkey, but attend away, or walk away from the monkey, but attend to the monkey. The cell may not have responded to these motion types, as the end goal of the motion would be different, e.g. monkey receives a reward.

7.3.3 Histological reconstruction

Histological data is not available from subject Steve as this monkey is still being used in ongoing neurophysiological and behavioural experiments. The reconstruction of cell postions within subject Esther (see Chapter VI for methods), indicated that cells responsive to the stimuli discussed in this chapter were located in the upper and lower banks of the anterior STS (see Figure 7.22).

7.4 General Discussion

The responses of cells reported in this chapter confirm earlier studies (Perrett et al 1985a, b, 1989a, b, 1990a, b, c, 1991, Oram and Perrett 1994, 1996, Wachsmuth et al 1994) which suggested that the STS is one area of the monkey brain which may code for the visual analysis of other's behaviour. Perrett and Emery (1994) also suggest that the responses of neurons selective to cues of another's attention may be used to analyse another's behaviour within a purposive framework. It is difficult to completely support or refute claims of this type when the sample of cells presented are small.

The responses of the cells described in this chapter may be explained in a number of ways, but a social interpretation makes the most sense. In order to survive, a monkey

Figure 7.22. Histological reconstruction: Attention and intention (static). **(a)** Series of frontal sections of the STS every 1mm (6.5 {bottom}to 5.5mm {top} anterior in the interaural plane) reconstructed from one monkey (E) showing the location of cells responsive to static view (open circles), view and orientation (filled circles), head elevation (open triangles) and eye gaze (filled triangles).

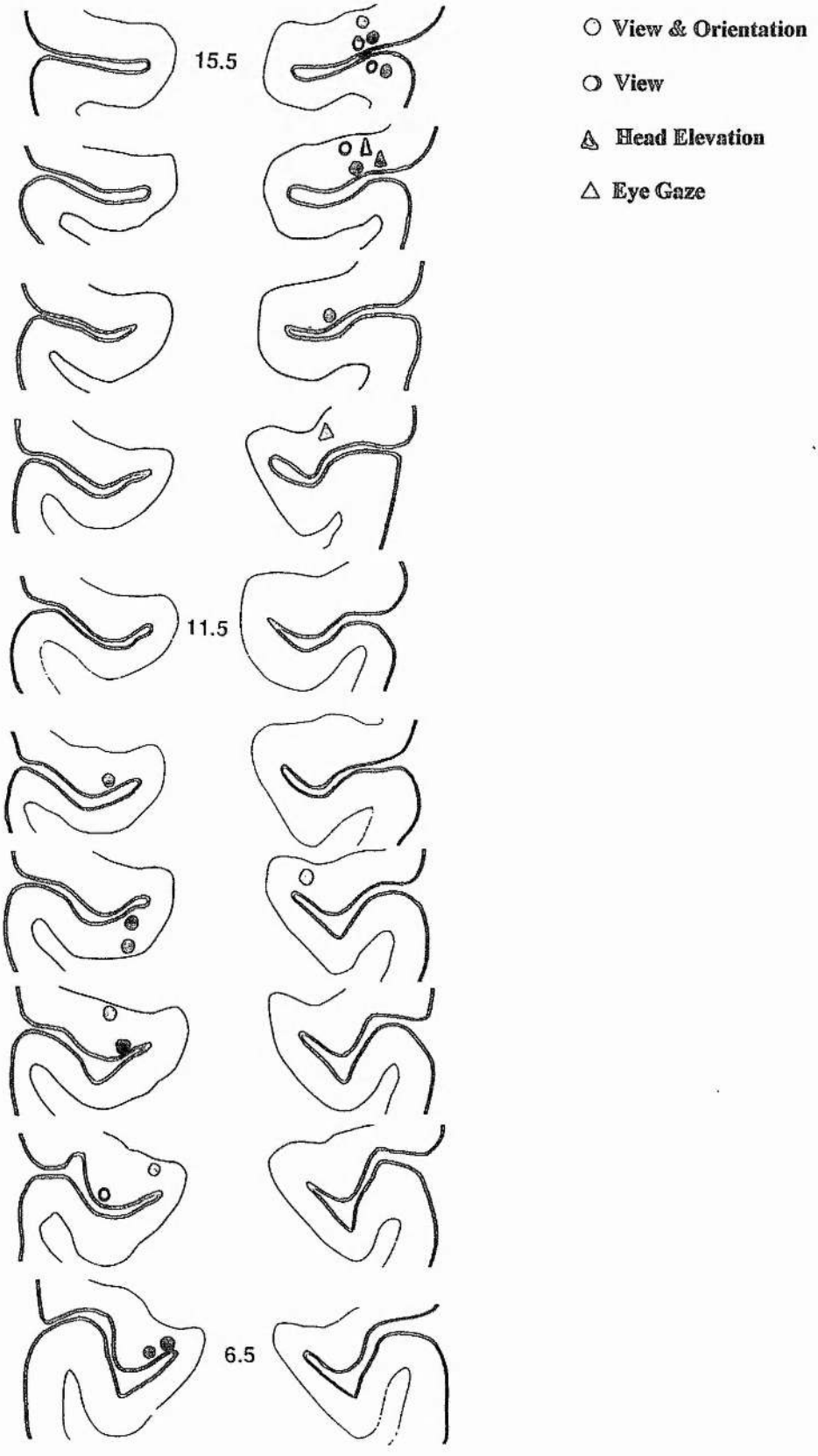


Figure 7.22. Histological reconstruction: Attention and intention (motion). (b) Series of frontal sections of the STS every 1mm (6.5 {bottom}to 15.5mm {top} anterior in the interaural plane) reconstructed from one monkey (E) showing the location of cells responsive to view specific, direction non-specific motion (filled circles), direction specific, view non-specific motion (open circles), direction and view specific motion (open triangles) and interactions with objects (filled diamonds).

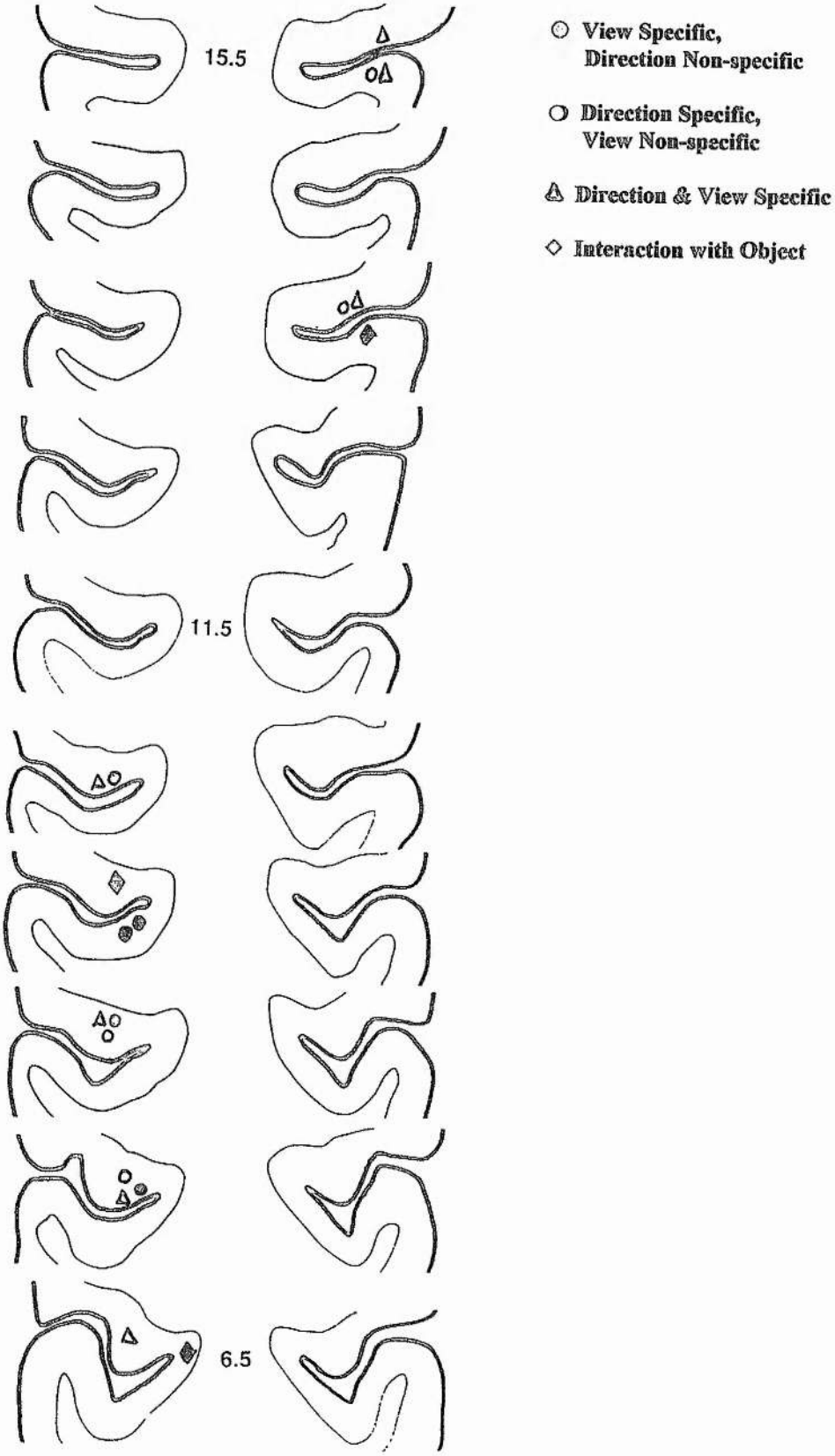
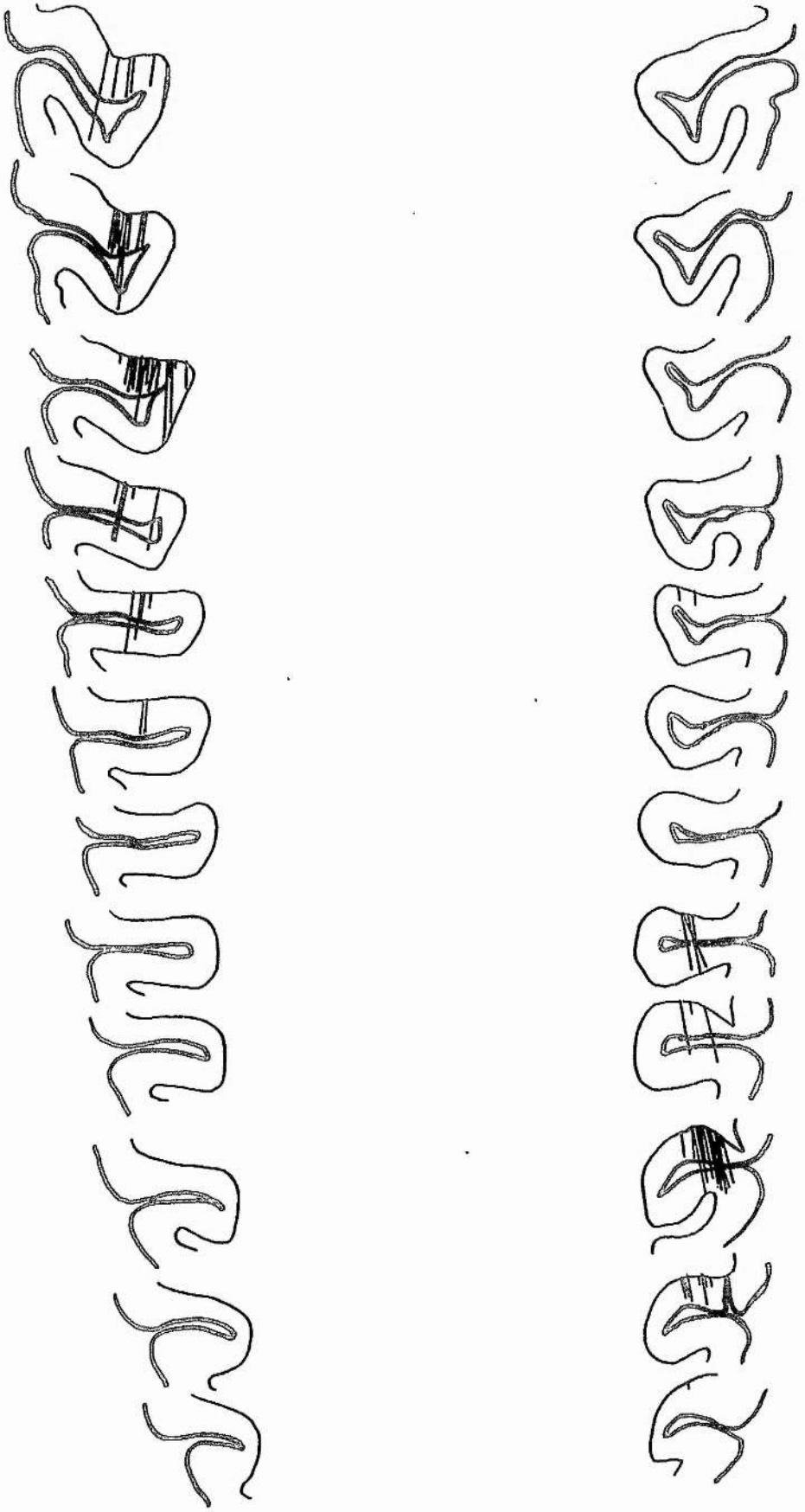


Figure 7.22. Histological reconstruction: Attention and intention (static and motion). (c) Series of frontal sections of the STS taken every1mm (6.0 to 17.0mm anterior in the interaural plane) reconstructed from one monkey (E) showing the location of recording tracks. Thick black lines indicate the surface of the cortex and the thin black lines indicate the boundary between white and grey matter.



or ape must have intimate knowledge of their environment (such as good sources of food and water, where to get them in times of hardship, and the probable location of predators and how to avoid them), but also how to interact appropriately with conspecifics. Theory of mind has been proposed as a method which enables humans to function successfully in the social domain (Baron-Cohen 1994, 1995). Evidence suggests that this domain-specific system may not be available to non-human primates (particularly the Old and New World monkeys, lesser apes and prosimians). (There have been no studies of lesser ape theory of mind, but as the evidence for great ape theory of mind is controversial, the capacity of lesser apes is as likely to be controversial.) The same evidence indicates that non-human primates can read another's behaviour, rather than another's mental state (Cheney and Seyfarth 1990a, b, c, 1991, 1996). The form of behaviour-reading that non-human primates may employ, may not require that mental states are read (as proposed by a theory of mind). Predicting what another individual animal will do next (within a sequence of actions) does not require that mental states need to be attributed to the observed animal. Experience forms a large part of interpreting another's future behaviour (X always does Y, so X will do Y again in the same situation.). This form of analysis does not require higher-order levels of interpretation beyond complex behaviour reading. This level of analysis is, however, more complex than the methods with which the majority of animals may respond to the behaviour of conspecifics (i.e. within a behaviourist framework, see MacPhail 1987, 1996). For example, individual W performs behaviour X and this effects behaviour Y of individual Z. Individual Z does not attempt to change the outcome of individual W's behaviour X, so thata different behaviour V occurs. Animals may always respond to a particular stimulus with a particular action.

Humans do not always successfully interpret what another's attention, goals, beliefs, etc. are going to be. Attributions of mental states are not always correct, as humans (and may be other primates) are not mindless automatons reacting to changes in the environment, which may easily be predicted (e.g. X has occured, so Y will do Z; if Q occurs, Y will do R).

The introduction to this chapter discussed the possible ways with which monkeys and apes may analyse other's behavioural patterns and interpret purpose behind their

behaviour (in a non-mentalistic fashion). The cells reported in this chapter fit with this interpretation. Observing the goal of another's use of a tool and how actions with tools interact with objects, requires not only an understanding of another's actions, but also how those actions can be integrated into the observer's behavioural repertoire. For example, tools may not have been used prior to the observation of a conspecific using a tool. The physical capability to use the tool may be present in the animal's physical repertoire (e.g. the correct grip). Matching the observed action with an exact brain record of the precise physical ability required to perform the novel, observed actions using the tool in the approriate manner, would be required . For example, a chimpanzee infant observes his mother using a stripped twig to fish for termites (Goodhall 1971). The infant has the physical capability to perform the same action; hands and neuromotor system for producing the same actions as related to the twig and the termite mound. To perform the same action, the infant's brain must match the existing visual neural records for this action (as observed from the mother's actions) with the motor output required to perform the correct action (visuomotor transformation). Neurons coding the sight of actions onto objects (or simple interactions with objects) would be an important and integral step to forming mental representations of observed actions. These forms of representations may be formed in premotor cortex by 'monkey-see-monkey-do' neurons (Carey 1996) which code for the appearance of actions on objects and the motor output of the same actions (Gallese et al 1996, Rizzolatti et al 1996), which are obviously of importance when discussing mechanisms of imitation.

Chapter VIII

Neuronal Categorisation of Primate Species

"Individual recognition requires that animals form mental representations of the properties of conspecifics as well as of the identity of particular conspecifics. These representations should be neurally encoded, stored in plastic areas of the brain, and reactivated when recognition occurs."

Zayan (1994, p. 233).

8.0 Summary

Earlier chapters have distinguished the anterior temporal cortex as an area which contributes to social behaviour (in particular the perception and recognition of facial stimuli and social signals). The goal of this chapter is to examine whether cells responsive to faces are sensitive to species differences. Different cells within this region were found to respond preferentially to human faces or preferentially to monkey faces. Other cells were unselective, responding to both monkey and human faces. The results are discussed in terms of species recognition at the behavioural level and the natural categorisation of primate species at the neural level. Some cells also responded preferentially to monkey body parts and other cells were sensitive to the eye positions of the observed monkey head (see also Chapter VII). The results of this chapter have important implications for the results of Chapter IX, where recognition of social signals may be enhanced or present only when cues are displayed by the same species (rather than cues from humans).

8.1 Introduction

8.1.1 Ethology of Conspecific Recognition

Evidence exists for species (and individual) recognition in a large number of invertebrates and vertebrates (Fletcher and Michener 1987). Monkeys and apes appear to have the ability to distinguish between the subtle differences of similar species, at the behavioural level. As with other forms of social communication, diurnal anthropoid primates employ predominantly visual and vocal methods in conspecific recognition. This small review will discuss only the role of vision in recognition.

There are three possible *levels* of recognition which a particular individual can achieve. First, recognising that an individual is part of a larger *category* such as species (e.g. *Macaca mulatta* or *Macaca fascicularis*), genus (e.g. *Macaca mulatta* or *Papio anubis*), subfamily (e.g. *Cercopithecinae* or *Hominoidea*), order (e.g. *Primate* or *Insectivora*) or class (e.g. *Mammalia* or *Aves*). Second, recognising that an individual is kin (e.g. mother, father, siblings). Finally, distinguishing the exact identity of the observed individual (e.g. mother, alpha male, best friend, Uncle Joe, etc.).

(a) Species recognition

Individuals must be able to recognise other members of their own species, or else they would not be able to mate or socially interact. This is beyond doubt. Do individuals, however, distinguish own species from closely related species, or from distantly related species using simple perceptual cues, such as face and body shape?

Fujita (1990, 1993a) studied the preferences of infant Japanese and rhesus macaques when presented with pictures of different or same species. All subjects were separated from their mother 7 days after birth and then human reared. During rearing, the infants were either caged with an age-matched individual of the same species or an aged-matched individual of a different species. For testing, the infants were trained to press a lever when a bulb illuminated, which would cause a picture to appear on screen.

Preference for the picture was scored as the length of time before the lever was pushed again to present a different picture. The subjects were tested at 3, 6, 9 12, 18 and 27 months old. The stimuli were slides of rhesus and Japanese macaques, either including or not including infants. Rearing condition (same species versus different species) did not seem to effect the overall preference of the subjects. All subjects appeared to prefer slides of rhesus macaques. An older Japanese macaque trained in a similar way, preferred adult Japanese macaques over adult rhesus macaques. There may be an effect of rearing condition on species preferences in Japanese macaques.

In a third experiment, 14 month old rhesus and Japanese macaques were presented with slides of Japanese, rhesus, Taiwanese, crab-eating, pigtail, bonnet and stumptailed macaques, either with one, two or more than two animals of the same species in each picture. Rhesus macaques preferred their own species; rhesus and Japanese macaques showed a negative preference for crab-eating and stumptailed macaques and Japanese macaques showed a strong preference for pig-tailed and bonnet macaques. When rhesus and Japanese macaques were cross-fostered (Fujita 1990), the Japanese infant reared by a rhesus mother, preferred slides depicting scenes with rhesus monkeys, but there was no clear statistically significant preference of rhesus infants reared by Japanese mothers (although the tendency was a preference for rhesus). A preference for rhesus macaques in Japanese macaques may be innate. Delson (1980) has suggested that Japanese macaques were derived from rhesus macaques who immigrated from Asia to the Japanese islands in the Middle Pleistocene period.

The same species preference with adult rhesus and Japanese macaques was replicated in normally reared pig-tail macaques (Fujita 1993b). Adult monkeys were tested using a similar paradigm as previously and responses to pictures of Japanese and pigtail macaques (either with the whole body or with parts removed) were measured. The subjects clearly preferred their own species. The preference for the pig-tail pictures was reduced if the head and tail, or just head were removed from the pictures. There were no changes in preference when the tail only, body only or background were removed. Pig-tail macaques preferences, therefore, appear to be based on a combination of body features (including the head), not just single features.

Dittrich (1994) also studied which physical features monkeys appeared to be use in their discrimination of other species and found contrasting results. In tests, subjects (long-tailed macaques) were not examined for preferences, but subjects had to discriminate pictures of a previously learnt vervet monkey from pictures of a baboon, a patas monkey and a cebus monkey. All the stimuli were presented simultaneously and the subject had to press a button next to the picture of the vervet monkey. The pictures presented were either whole body, torso without head, head alone, extremities (legs and arms), head and extremities, and torso and extremities. Subjects were proficient in discriminating the vervet from the other species and appeared to be making discriminations based on the presence of the torso (with and without extremities). The head was not required for discrimnation, as in the Fujita (1993b) study. Monkeys may *prefer* the head (as the face provides large amounts of social information), but monkeys may make *discriminations* between species on the presence of other body parts.

The preference for same species seems to be present in the preferences of other species of macaque. Fujita and Watanabe (1995) studied the preferences of seven closely related species of Sulawesi macaques (*M. nigra, M. nigrescens, M. hecki, M. tonkeana, M. maurus, M. ochneata, M. brunnescens*). There is probably extensive interbreeding within these species and the differences between the species are very subtle. All seven species, when tested using a similar preference paradigm to Fujita (1990, 1993a,b), clearly preferred pictures of their own species.

Monkeys also appear to be proficient in discriminating between species of non-human primates and non-primate vertebrates (birds, ungulates, carnivores, etc.). Preference time was measured for stump-tailed macaques watching slides of different animals for 15 minute trial periods (Demaria and Thierry 1988). The subjects preferred slides of stumptailed macaques and slides which included adults with infants (greater preference than slides with infants only or adults only). Duration of fixation was greater for mammals than for birds, with felids (cats) examined more than ungulates (cattle) and canids (dogs). Demaria and Thierry suggested that felids' eyes were important and tested differences in preference between mammalian species with forward facing eyes or averted eyes. The eyes appeared to make no differences to the preference of felids over other

mammals. It is possible that there is an innate interest response to felids, which are naturally predatory to monkeys.

The majority of behavioural work conducted to test species (and between classes, orders, subfamilies, genus's, etc.) discrimination has been performed by experimenters investigating primate's categorical perception of objects. Monkeys have a natural interest in pictures of animal over pictures of country scenes (Humphrey 1974). Schrier and Brady (1987) have suggested that the interest may be because monkeys categorise objects individually rather than as collections of objects as multiple parts of a whole scene. Animals, although collections of objects themselves (such as body parts), are different from scenes, which by nature, have thousands of small details which would be impossible to categorise at the individual level. Categorising pictures individually takes longer to process, by fitting percepts with specific exemplars within a category (i.e. all monkeys have tails, faces, a body, four legs, etc., but stumptailed macaques have short tails, rhesus macaques have medium-sized tails, long-tailed macaques have long tails, etc.). Interest in a stimulus may be highly correlated with time spent inspecting the stimulus.

Yoshikubo (1985) tested the proposition that rhesus monkeys form *concepts* about other species, based on their common attributes. Subjects had to spontaneously discriminate between pictures with and without rhesus monkeys (of varying size, distance from the camera and horizontal view). Three lights were illuminated simultaneously with the presentation of pictures. When a key was pressed, a reward was delivered (S+). If a key was pressed when the lights were not illuminated (during simultaneous presentation of a picture), the subjects were not rewarded (S-). Pictures with rhesus monkeys were S+ and pictures without rhesus monkeys were S-. The subjects performed these discriminations after an average of 10 sessions (80 trials per session). Next, the subjects made discriminations between pictures of rhesus monkeys and other animals (humans, chimpanzees, dogs, pigeons, sheep, snakes, etc.). Finally, the subjects were able to discriminate between Japanese and rhesus monkeys.

Monkeys can also distinguish between slides which include humans and slides in which humans are not present. D'Amato and Van Sant (1988) trained two capuchin

subjects on a slide set of human exemplars (a collection of pictures of humans with similar shape, size and build). Choice of the human slides was reinforced by rewarding the subjects each time a slide with a human was chosen, above other slides of scenes without humans. This scenario was switched for the second subject; i.e. choice of humans was unrewarded. Both subjects were then asked to perform a transfer task on a novel set of human slides. Both subjects achieved a significant transfer in a relatively small number of trials. A second set of capuchin subjects were tested to determine whether the transfer effect remained if the skin-colour of the humans in the slides was changed. Skin-colour did not significantly effect discrimination of humans from other slides. Rhesus monkeys can also make these discriminations after a large number of trials (and training) and can distinguish humans from non-human primates (monkeys and apes), even when the human pictures are scrambled and inverted, but not when they are silhouetted (Schrier and Brady 1987).

Schrier et al (1984) previously found that rhesus monkeys could be trained to choose scenes including humans from those that did not and to transfer this ability to novel slides. The choices of the macaque subjects were not made by analysing individual slides. This is in contrast to Schrier et al's later findings. Schrier et al (1984) also tested stumptail macaques in the same experiment (choice discrimination), but tested for categorisation of non-human primates from other animals. The stumptail subjects could distinguish between slides of different animals (primates versus non-primate animals), but transfer to novel pictures appeared to be difficult, unless the slides were of macaques. A single stumptailed macaque, however, made high percentage correct transfers for humans and monkeys when using a go/no-go procedure, rather than a choice discrimination procedure. The results, therefore, may be dependent on the method of testing, on individual performance, or on the amount of previous experience of the categories being tested.

When presented with pictures of a number of primate species (monkeys, apes and humans), outdoor scenes and other objects (flowers, trees, fruits), rhesus monkeys' responses, on a same/different picture task, were similar for primate pictures and for other objects (in the majority of cases). Interestingly, one subject grouped an outdoor

scene (blue sky), a blue flower and a mandrill (blue face) together, which all have some blue features. This subject may have been grouping using a simpler concept of the colour blue, rather than classes of object. Monkeys, may use a concept of primate, not just individual species (Sands, Lincoln and Wright 1982), but also lower levels of conceptual analysis (such as colour).

The results described above suggest that there are innate abilities to distinguish between same species and other closely related species. The ability to differentiate primates and humans from other objects was demonstrated only after extensive training. The use of different testing methods, reflecting subtle changes in recognition, may reveal spontaneous abilities of species discrimination. The results of the above studies do not tell us how monkeys categorise same and other species in their natural environment. Cheney and Seyfarth's studies of vervet alarm calls provide evidence that monkeys do form concepts about different animals (see Chapter II). As stated in Chapter II, vervets use at least three different alarm calls in response to the sight of different types of predator (Seyfarth et al 1980a, b, Cheney and Seyfarth 1990c). Vervets probably have at least a general concept of predator (an aversive, dangerous, external, animate stimulus) and more likely, concepts of multiple types of predator (avian, large mammal, snake). The use of specific alarm calls would be redundant without such concepts. Use of different alarm calls for different predators (eliciting different, appropriate responses from conspecifics) provides evidence for multiple concepts of predator in vervets (Seyfarth et al 1980a, b).

(b) Kin recognition

Kin are probably not recognised just by basic perceptual signals based on the physical features of an individual. Other perceptual cues may be utilised. For example, kin are often found within close proximity to one another (Gouzoules and Gouzoules 1987). This is particularly apparent for mothers and infants, and aunts/uncles and cousins to a lesser extent. Rates of grooming may also be higher between kin.

Some authors have recently suggested that kin recognition in monkeys may be attributed to familiarity only (Fredrickson and Sackett 1984). Fredrickson and Sackett

(1984) attempted to replicate an earlier study (Wu et al 1980), where infant pigtailed macaques displayed a trend (non-significant, p=0.1) to select genetically related males over unrelated males. Frederickson and Sackett studied the preferences of a larger sample of infant macaques of adult males of varying familiarity and relatedness to the infants subjects. Fredrickson and Sackett did not find the trend shown in the previous study. There was no effect of genetic relatedness on social preference for individual males. Preferences may have been based on familiarity cues only. This may certainly be the case for related males, including fathers, as there is little or no form of parental contribution to an infant's welfare after conception. There is little benefit to the infant to maintain links with their father. The bond between mother and infant, however, is different and is due probably to aspects of kin recognition which cannot be attributed just to familiarity. No reasonable length of time would have passed between birth and preliminary contact with the mother to establish familiarity (this would not explain the initial attraction of the infant for the mother). Familiarity does not breed contempt for infants towards their mothers.

(c) Individual recognition

Individual recognition by primates has not be overly studied despite the importance of this every-day behaviour. For example, knowledge of an individual's position in a dominance hierarchy is vital for conflict avoidance. (Note: amygdala lesions may cause disruptions in responding appropriately to an individual's threatening gesture, when that individual is more dominant. This may either have been due to a deficit in coding the significance of the threat expression {the emotionality was removed from the basic perception of the threatening face} or a deficit in correlating the act of a threat with the dominance of the individual providing the threat, i.e. not linking "X is threatening me and X is dominant to me, therefore I should respond with a submissive gesture".)

A new-born infant must begin to recognise individuals as soon it is born. Whether this form of recognition is visual, auditory, tactile or olfactory is not known. The infant may attach itself to the first animate object in its immediate proximity, but it is more likely that the mother naturally nurses the infant until the infant reaches a point in

development where it can discriminate objects visually. Rodman et al (1993) found that cells selectively responsive to faces could be successfully recorded in inferotemporal cortex (IT) and the superior temporal polysensory area (STP) of 2 month old infant rhesus monkeys. An interesting experiment would be to determine differences in response between pictures of the mother versus other familiar and non-familiar monkeys. Face-responsive neurons in the amygdala may differentiate based in hedonic (emotional) value of the mother's face compared to unknown faces. Behaviourally, 12 week old Japanese macaques can discriminate their mothers from three unfamiliar females (Nakamichi and Yoshida 1986), when proximity, speed of approach and orientation are taken as measures of the infant's preference.

Chimpanzees and orangutans would be expected to recognise individuals, as they can distinguish reflections of themselves in mirrors as being distinct from conspecifics (Gallup 1970). Recognising the self as an individual distinct from others, may be an advanced form of individual recognition (Gallup 1970, 1982). Monkeys and gorillas do not appear to recognise themselves in mirrors (Povinelli 1987 for review, although see positive results for a New World monkey; cotton-top tamarin in Hauser et al 1995). This does not mean that monkeys and gorillas have deficits in individual recognition as they may still recognise other individuals from their vocal or olfactory signals, or may class others by their appearance, whilst having no knowledge of their own physical features. (The complex arguments surrounding self-recognition, the mirror test and connections to discussions about the presence of a non-human primate theory of mind will not be discussed here, but the reader is directed to various discussions; Gallup 1982, Povinelli 1987, Heyes 1993, 1997.)

Chimpanzees tend to differentiate individuals by physical features. Boysen and Bertson (1986) displayed slide photographs of familiar human caregivers, familiar individuals, strangers and control slides to a 3.5 year old female chimpanzee. Electrodes were attached to the chimpanzee to measure heart rate before, during and after presentation of the photographs. The subject's heart rate changed in response to all photographs, but the largest change (decrease) and variability in heart rate response was apparent when the subject looked at pictures of caregivers. The emotional response

associated with this decrease in heart rate correlated with the identity of the human caregiver (who provides food, water, social bonding, etc.). The same subject was also presented with pictures of conspecifics, who were either friendly and familiar, aggressive and familiar, or unfamiliar (Boysen and Bertson 1989). Heart rate was measured again and an accelerated response was associated with the aggressive chimpanzee, a deceleration with the unfamiliar conspecific and a minimal change with the friendly chimpanzee. The subject was therefore able to, not only recognise individuals, but also to link subjective feelings with these individuals.

Monkeys and apes also classify conspecifcs dependent on previous social interactions and social history. Female baboons, for example, appear to produce long-term bonds or friendships with other females and males (Smuts 1985). This form of behaviour is ultimately dependent on recognising an individual from physical features and linking basic perceptual details with information about an individual's social history, such as whether the individual aided the observer in a previous aggressive encounter. Such friendships provide many benefits such as relaxation and comfort (from females) and protection (from other males and predators) and increased access to preferred foods (Smuts 1985, Cheney et al 1986).

Dasser tested long-tailed macaque's ability to recognise kin associations in the laboratory. First, Dasser trained the subjects to respond to one of a pair of simultaneously presented pictures of unknown individuals or family members (Dasser 1987). The subjects then had to transfer to a novel set of stimuli, which included familiar individuals (not seen in training) or novel slides of animals used during training. During the transfer trials the subjects correctly discriminated 44 out of 60 slides of familiar individuals, but only 7 out of 18 unknown animals. In a matching-to-sample task, the sample slide was a familiar animal. The subject was then presented with an identical or similar slide of the same animal or a slide of a different animal. The subject was able to successfully match to the sample when novel slides of the face, novel slides of the whole body and slides of non-overlapping body parts were presented (e.g. face and feet).

Long-tailed macaques were also able to determine social relationships from slide representations (Dasser 1988). First, the subjects were trained to respond to pictures

with pairs of animals versus not to respond to pictures with single animals. Then, using similar paradigms to above, the subjects had to transfer to pictures with novel combinations of previously seen animals or novel animals. In the discrimination experiment, one subject were presented with two slides, one with a mother-infant pair, the other with unrelated female-infant pairs. The subject correctly identified all 14 of the mother-infant pairs. In the matching-to-sample experiment, a second subject was presented with a sample (mother) and two choices (offspring or a similar infant). The subject also performed well, matching 20 out of 22 infants with their mothers. This effect was reduced, however, when the infants were 2-3 years older (10 out of 16 correct).

8.1.2 Neurobiology of Conspecific Recognition

If monkeys have the behavioural capacity to distinguish between closely related species, kin and individuals, some system in the brain must be driving these processes of recognition. Cells which are responsive to faces have been described in many parts of the monkey brain (see Chapters II and VII). The response of face-selective cells is usually to the presentation of human faces, however, some studies have tested cells with non-human primate faces. In one of the first full accounts of face-selective cells, Desimone et al (1984) reported a number of cells in inferotemporal cortex which either respoded to photographs of monkeys and photographs of the experimenters. The stimuli were used interchangeably, not simultaneously, i.e. the differential effects of species on cell response was not tested. Perret et al (1984) reported that the responses of a small number of cells were greater to monkeys compared to humans. Rolls (1984) used pictures of monkeys (with neutral and threatening faces) to elicit responses from cells in the STS and amygdala. (Cells tested for response to different facial expressions were tested mainly with monkey stimuli; see Chapter II.)

Cells responsive to faces have also been found within comparable areas of the temporal lobe of sheep (Kendrick and Baldwin 1987). The responses of these cells were dependent on the species of the animal face. Kendrick (1994) presented faces of different types of sheep, such as those with long or short horns, curved versus straight horns, etc.

and some cells differentiated between categories. Other cells responded to sheep dogs and humans, but the majority preferred pictures of the same breed.

Perrett et al (1984) found a small subset of neurons in the STP which were specific for the identity of two particular human experimenters. Hasselmo, Rolls and Baylis (1989) found that the responses of cells in the inferior temporal gyrus were affected by the identity of three individual monkeys. Three different facial expressions were also tested, with expression and identity effecting cell responses depending on the cell location (STS; facial expression or IT; identity).

None of the studies to date, in macaques, have tested the response of face-selective cells to more than two species. The studies which have tested responses to specific monkey and human faces (Desimone et al 1984, Perett et al 1984, Rolls 1984, Young and Yamnae 1992) reported comparable responses to humans and monkeys for the majority of cells (but see Perrett et al 1984). The studies in sheep tested at least three species; sheep, sheepdog and human (Kendrick 1994). The behavioural evidence discussed in section 7.1.1 suggested that monkeys can diffferentiate between the sight of a number of different animal species. It is probable, that the process of species recognition can be localised to populations of single cells within the anterior temporal cortex.

Disorders of human face identity recognition, such as prosopagnosia (Damasio 1985) and Capgras syndrome (Hirstein and Ramachandran 1997) occur through brain trauma (organic or surgical). Prosopagnosia is a form of agnosia restricted to face recognition; where recognition of previously familiar faces is either disrupted or completely absent (Milders and Perrett 1993). This disorder can develop after unilateral damage to the occipto-temporal region of the fusiform gyrus (Damasio 1985). Recently, neuroimaging and electrophysiological studies in humans have revealed significant levels of activation in the midfusiform and inferior temporal gyri to the presentation of face-stimuli (normal and scrambled; Allison et al 1994, Puce et al 1995). Failure to identify previously known faces has also been shown in some patients with bilateral amygdala damage (Young et al 1995).

Capgras syndrome is a misidentification syndrome. Patients suffering from this disorder do not suffer from prosopagnosia, but fail to attribute the correct emotional valence to the faces they can recognise (Hirstein and Ramachandran 1997). Capgras syndrome is similar to the delusions of people in the movie, "*Invaders of the Body Snatchers*". The patient recognises family and friends but suggest that they are "impostors" and are not really who they look like. Hirstein and Ramachandran (1997) have suggested that Capgras syndrome may be attributable to a disconnection of the inferior temporal cortex with the amygdala, or damage to the right fronto-parietal cortex.

Attempts to produce prosopagnosia in monkeys has so far failed (Heywood and Cowey 1992). The monkeys were tested on discriminations of familiar from non-familiar individuals and pre-operatively the monkeys were good at this discrimination. Bilateral lesions of the STS were performed (due to the large number of face responsive neurons found within the STS), but deficits in face-recognition (such as discriminating familar individuals) were not seen post-operatively. Right temporal lobe damage is sufficient to cause prosopagnosia in humans. Monkeys do not have lateralisation of function, i.e. both hemispheres perform the same function, whereas in humans each hemisphere performs a different function. Bilateral damage, therefore, would be required to effect face-processing, but this causes deficits in other forms of processing, such as object recognition (Perrett et al 1992, Milders and Perrett 1993).

It would have been interesting if Heywood and Cowey (1992) had tested monkeys with pictures of extremely familiar monkeys (such as siblings, alpha male or breeding females), rather than pictures of novel monkeys, which were learnt briefly pre-operatively. This could be achieved by choosing subjects within an established social group, where pictures of individuals could be easily obtained.

8.1.3 Aims and predictions

The ability to recognise a class of animate/biological objects as conspecifics or distinct individuals within a species is vitally important for a social animal. Recognising

an animate object as belonging to the class 'dangerous animal' or predator requires a similar level of recognition to recognising a conspecific. Primates may categorise animals by matching percepts of objects, with templates of previously observed examples or templates present from birth, e.g. object X matches the template for predator. Recognising another individual as being a conspecific requires a further level of processing (is the conspecific kin?, what is the identity of the conspecific?, what is the conspecific's social history?). Chapter II discussed certain brain regions that may have evolved to process information utilised in social relationships. The first step in evaluating social signals provided by another individual is recognising that the other individual is of a specific category with which interaction is possible (i.e. specific species, kin or individual). It is invalid and inappropriate to attempt to socially interact with a species which can not understand or act appropriately to species specific social signals.

The purpose of this chapter is to examine the responses of neurons within the cortex of the STPa which are sensitive to the differences between distinct animal species, humans and monkeys. The function of these particular type of cells may be for species recognition. The cells may also be precursors to the types of cells described in Chapter VII, which are responsive to more complex forms of social interaction (such as motion, attention and action).

It is predicted that the responses of face-selective cells within this brain region may respond in three ways, dependent on the test used. Previous authors have described the responses of face-selective neurons to human and monkey faces. A number of cells may respond to either monkey or human faces (as both species are equally salient to laboratory primates). Humans provide food, but are also aversive stimuli. Conspecifics provide opportunities for social interaction, including copulation. Some neurons may respond only to the sight of monkey faces (when tested with human and other animal faces). The responses of these neurons would reflect a high level of species recognition.

Some neurons may also respond only to the presence of human faces (when tested with monkey and non-primate animal faces). The responses of these neurons would also reflect a high level of species processing. The responses of a further collection of cells may correspond to the category of *primate face*, i.e. cells may respond to the

sight of all different primate faces, including human and monkey faces. Primate faces are similar in features and the configuration of features (see Chapter II) and may be classed together as similar objects. Other non-primate animal faces are physically different from primate faces and therefore, may be classed differently to primate faces.

It is also predicted that some cells may respond equally to the presentation of all faces (independent on species). The responses of these neurons would reflect coding faces as a broad category of object, which would be at a lower level of recognition. Cells coding for faces as a category of objects should respond equally to all species where a face, in a normal configuration, is presented. The predictions made above can be made, not only for faces, but also for body parts. The responses of numbers of cells selective for the front views of the head are dependent on the position of the eyes in relation to head view (Perrett et al 1992, see Chapter VII). Eye gaze is an important social signal for monkeys (see Chapters VII and IX). A final prediction is that the responses of a number of cells selective for monkey faces may also be dependent on the position of the eyes, as with the response of cells to human eye gaze.

The results of the previous chapter demonstrated that neurons within the STS were sensitive to head view, eye gaze and body parts. The responses of neurons were tested predominantly with human face and body stimuli. The studies described in this chapter were attempts to replicate the tuning characteristics of cells using monkey stimuli.

8.2 Methods

8.2.1 General methods

The general physiological methods are described in the previous chapter. Two subjects described in the general methods were used. Subject Esther for 6 months from January 1994 to June 1994 and subject Steve for 23 months from January 1995 to December 1996 (with 9 months break to take part in the behavioural experiment (see Chapter IX). Esther was used in previous neurophysiological experiments (from March

1993) and Steve is currently being used in neurophysiological and behavioural experiments. No anatomical data is presented for Steve because of his continued use in experiments.

8.2.2 Stimulus preparation

a) Static stimuli

Neurons were tested for their responses to static real 3D "junk" objects (such as toys, tools, foods, pieces of material, boxes, etc.), real 3D biological objects (heads and bodies of the experimenters) and 2D slide representations of the same biological objects. Static cells responsive to the head (face) were tested for response to different species (see Chapter VII for head responsive cells). Two basic species tests were produced onto slide. Slide stimuli were photographed using 200 ASA ectochrome slide film in a Nikon camera. Photographs were taken of colony rhesus and stumptailed macaque monkeys, with a either a dark background, or the cage as background. Monkey body parts were obtained in the same way. Slides of animal head and body stimuli were rephotographed from colour photographs in animal books and a guide to the San Diego Zoo. Extraneous details in the background were minimised by rephotographing the animal only. Other slides were created by removing digital images of animals off a CD-ROM containing animal photographs (Corel CD). Photographs of humans were taken using the same photographic set-up described for monkeys.

b) Testing methods

Every cell in which a clear continuous spontaneous activity (S/A) could be evoked, was tested with a variety of stimuli. The modality preferred by the cell was tested using junk objects, changing light levels, auditory stimuli (such as hitting objects, jangling keys, foot stamping, etc.) and tactile stimuli (stroking or grooming the monkey). Those cells found to be visually responsive were further tested (clinically) with a number of objects including faces and bodies, and faces and bodies in motion. Protocols using static slide stimuli of human and monkey faces, or monkey body parts were then used to

further study the precise response characteristics of the cell being investigated (see below for details).

1. *Animal faces.*

A cell's response to faces as a category of object were tested using photographic slide stimuli of faces of multiple species of animals. Cell responses were compared using slides of a wide variety of species, a series of control objects and S/A. A minimum test for species differences, used slides of two species of monkey (stumptailed and rhesus macaque), two individual humans, a hawk and different control objects. A larger test for species differences used a number of stimuli from a pool of slides of 27 different species of animal (including felids, canids, elephants, bears, frogs, birds, prosimians, monkeys, apes, insects and snakes) presented for only one or two trials each (see Figure 8.1 for examples of the stimuli). Intermediate tests used slides of smaller numbers of animal species, monkey body parts, random dot patterns, jumbled faces and different control objects.

2. *Human and monkey faces.*

A cell's differential response to human and/or monkey faces was tested using photographic slides of monkey and human faces. Cell responses were compared between monkey and human faces, a collection of control objects and S/A. A minimum test, consisted slides of a rhesus monkey face compared with one individual human face and a range of different control objects. A maximum test used slides of two species of monkey (stumptailed macaque and rhesus macaque), two individual humans and control objects.

3. *Monkey body parts.*

A cell's response to different monkey body parts was tested using photographic slides of monkeys' bodies, either presented whole, with the head only present (removed by occlusion), or with the body only present (also removed by occlusion). Cell responses were compared between head only, body only or whole body, different control objects and S/A. The body parts were presented in different horizontal views from the face (e.g.

Figure 8.1. Schematic representations of photographic slides used to test cell responses to different animal faces. Examples of photographs include stumptailed macaque, golden monkey, prosimian, hawk, gorilla, cheetah, parrot, toad, dog and lemur.

0^0, 90^0, 180^0or 270^0 from the front view), dependent on the maximal response of the cell, which was previously established. See Figure 8.2 for drawings of the monkey stimuli used to test the effects of view on responses to different body parts.

A cell's response to a large number of different monkey body parts was tested using photographic slides of monkey body parts tested in isolation. Cell responses were compared between head only, body only, whole body, hand only, top of the head, tail only, perineal region, face with the eyes closed, different control objects and S/A.

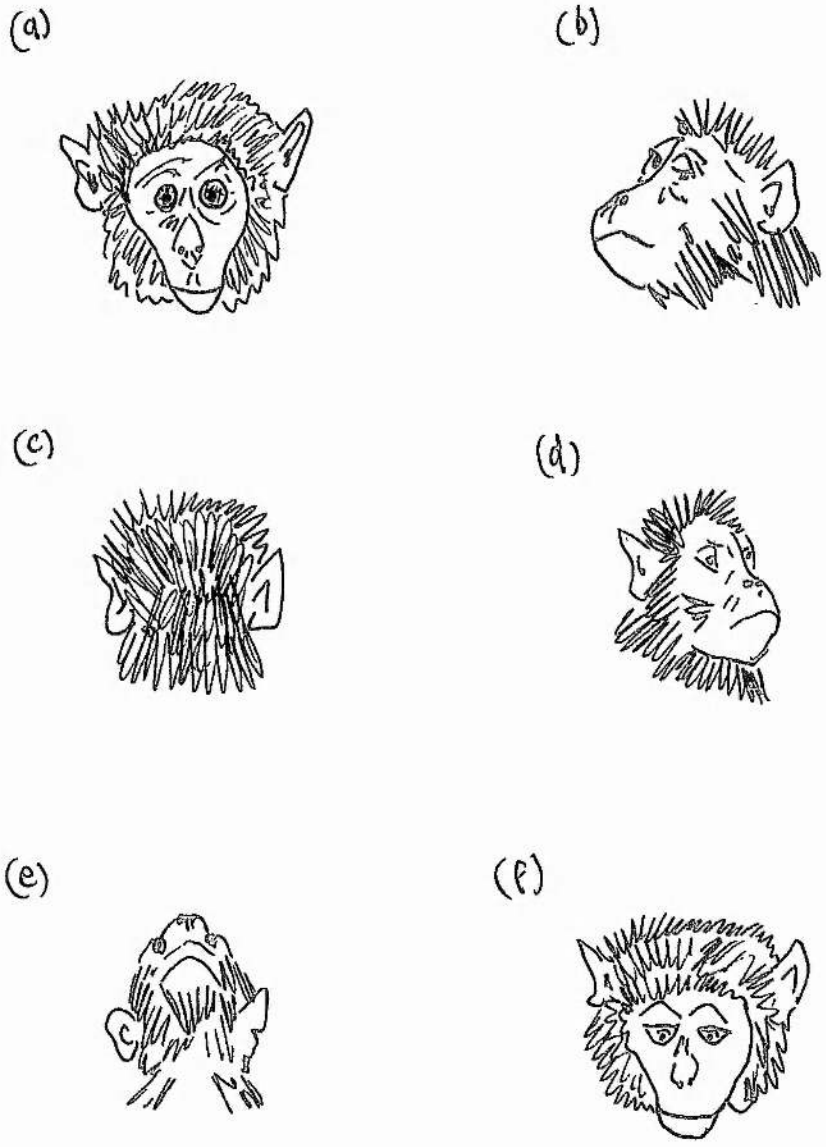
4. *Monkey eye gaze.*

Detailed protocols used to test for the effects of eye position on the neuronal responses to the sight of the front view of the human head (i.e. views 0^0, 90^0 or 270^0 from the face) were presented in Chapter VII. The sensitivity of the position of the eyes on cells responsive to monkey heads, were only tested with head view 0^0. Cell responses were tested using photographic slides of monkey heads with eyes forward (view 0^0 facing the viewer), eyes left of the viewer (view 45^0), eyes right of the viewer (view 315^0), eyes up, eyes down, different control objects and S/A.

c) Data analysis

Neuronal responses to the optimum presented species, were compared with other species, control objects and S/A using either one-way or two-way ANOVA's, and protected least significant difference, *post-hoc* tests to determine significant differences between conditions (PLSD, Snedecor and Cochran 1980). Cells were determined responsive to a stimulus if the cells responded to one or more of the stimuli presented, and the responses to the preferential stimulus were significantly different from S/A. Cells which did not respond to any of the presented stimuli were deemed to be inhibitory to those stimuli. In all cases, the results of the statistical analysis were plotted as histograms, displaying data as neuronal discharge during presentation of the stimulus (spikes per second).

Figure 8.2. Schematic representation of photographic slides used to test cell responses to different rhesus monkey head views. **(a)** monkey head view 0^0, **(b)** monkey head view 90^0, **(c)** monkey head view 180^0, **(d)** monkey head view 270^0, **(e)** monkey head view 0^0, elevation up and **(f)** monkey head view 0^0, elevation down.



8.3 Results & Discussion

8.3.1 General Response Characteristics

The general response characteristics of cells in the superior temporal cortex recording areas (for location of recording sites, see 8.3.3) are described thoroughly in Chapter VII.

8.3.2 Specific cell responses

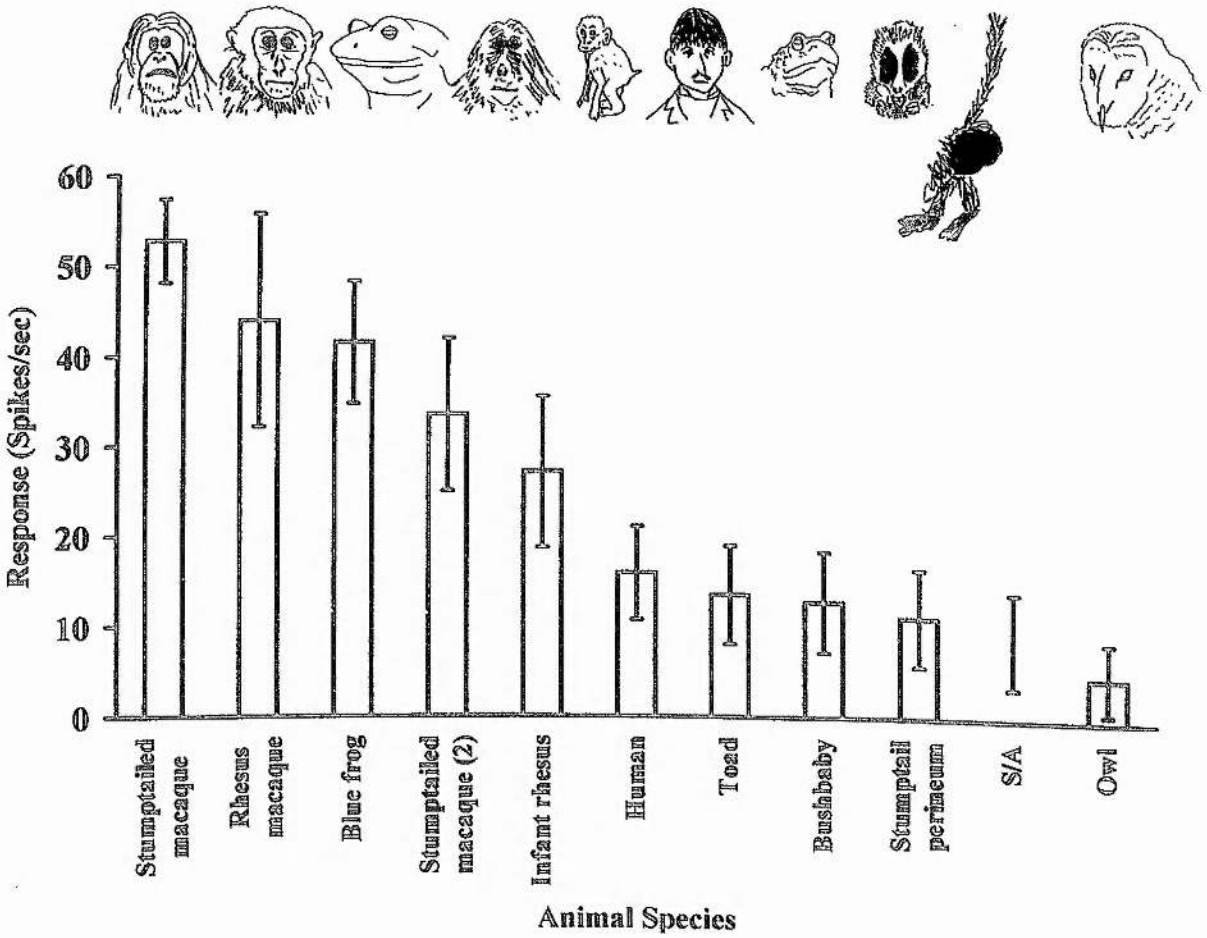
The responses of the visual cells were divided into two main categories; response to animal slides (this chapter) and responses to attention and intention cues (purposive behaviour, see Chapter VII).

1. Species

Twelve cells responsive to human faces were further tested for their response to a number of different animal species' faces (and bodies). One cell was broadly tuned to species face (see Figure 8.3). The cell was maximally responsive to stumptailed and rhesus macaques, but the responses to the monkey stimuli were not significantly different from the blue frog ($p>0.05$, PLSD). The responses to monkey stimuli were significantly different from the responses to human heads, a toad, a bushbaby, S/A and an owl ($p<0.05$, PLSD, all comparisons). A second cell (S49_2391) was tested for a larger range of species (mammals, birds, reptiles and amphibians; 27 species in total), with no clear responses to specific stimuli.

The response of cells which are broadly tuned for species (i.e. respond to a number of different species' faces) may be related to coding for the global object; faces, with differential responses between species of the face. All vertebrate faces have some common attributes; two eyes, two forward facing nasal openings (nostrils and a nose), a mouth and two aural openings (ears) on each side of the head. The position of the

Figure 8.3. Neuronal responses of a cell broadly tuned for different species' faces. Mean responses (+/- SEM, n=5 each category) to two stumptailed macaques, an adult rhesus macaque, an infant rhesus macaque, a frog, a human, a bushbaby, a toad, an owl, a stumptailed macaque perineal region and S/A for one cell (E82_3700). There was a significant effect of condition, ANOVA: $F(10,44) = 5.88$, $p < 0.00001$. Responses to the two stumptailed macaques, the rhesus macaque and the blue frog were significantly different from S/A (PLSD, $p < 0.05$, all comparisons).



features on the face may be different between species (e.g. the eyes may be on the side of the head instead of the front of the head), but the components of the face are universal for the majority of vertebrates.

Three cells were more responsive to monkey faces than human faces. One cell was highly responsive to the presentation of monkey stimuli compared to the presentation of human stimuli, with response greater than controls and S/A (PLSD, $p < 0.05$). The responses of this cell are displayed as a histogram in Figure 8.4. No other species (apart from monkeys and humans) were tested with this cell.

A second cell was originally tested for differences in the size of 3D heads and bodies where the chin was raised. The large and medium sized bodies were a model stumptailed macaque (large) and a toy monkey (medium). The medium-small and the small body were human dolls (all with movable parts). The cell was previously tested with a human (live presentation) raising their chin. The cell was responsive to the larger heads greater than the smaller heads, (PLSD, $p < 0.05$ all comparisons), with responses greater than controls and S/A (PLSD, $p < 0.05$). The cell was probably not responding to differences between the size of the objects, as the control objects (i.e. a broom head, a cereal box, a screwdriver handle, a plastic container and a piece of cloth, all moving upwards) were of a comparable size to the range of heads. The responses of this cell are displayed as histograms in Figure 8.5.

One cell (S52_2484) was tested for responses to monkeys, humans, hawks, controls and S/A. There was no significant main effect of condition, $F(8,36) = 2.01$, $p = 0.07$. The responses, however, suggest a difference between monkeys and humans.

The cell responses of the above cells appear to distinguish between different primate faces (although many primate species were not tested). Primate faces are more similar than faces of different mammalian orders or between different vertebrate groups. The processes used to distinguish between visually similar faces must be functioning at a high level of processing. The responses of these cells may be dependent on the subtle differences between monkey and human faces (recognition mechanism only) or the salience of the individual faces (recognition and emotional mechanisms). The latter proposition is possible due to the extensive connections between the STS and the

Figure 8.4. Neuronal responses of a cell sensitive to a monkey face compared to a human face. Mean responses (+/- SEM, n=5 each category) to a monkey head (view 0^0), a human head (view 0^0), control objects and S/A for one cell (E82_3700). There was a significant effect of condition, ANOVA: $F(3,16) = 26.16$, $p < 0.0001$. Responses to the monkey face were significantly different from responses to the human face, controls and S/A (PLSD, $p < 0.05$ all comparisons).

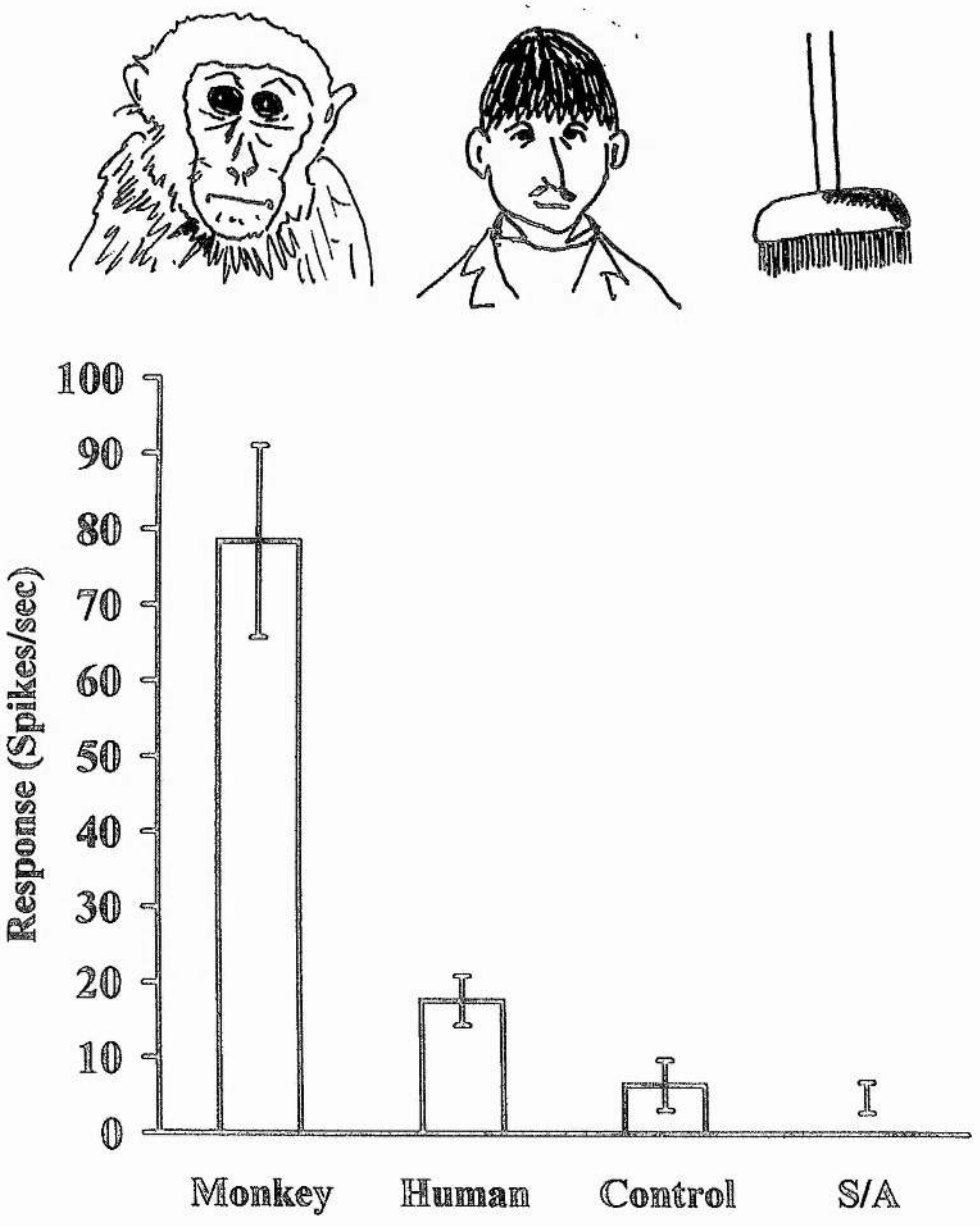
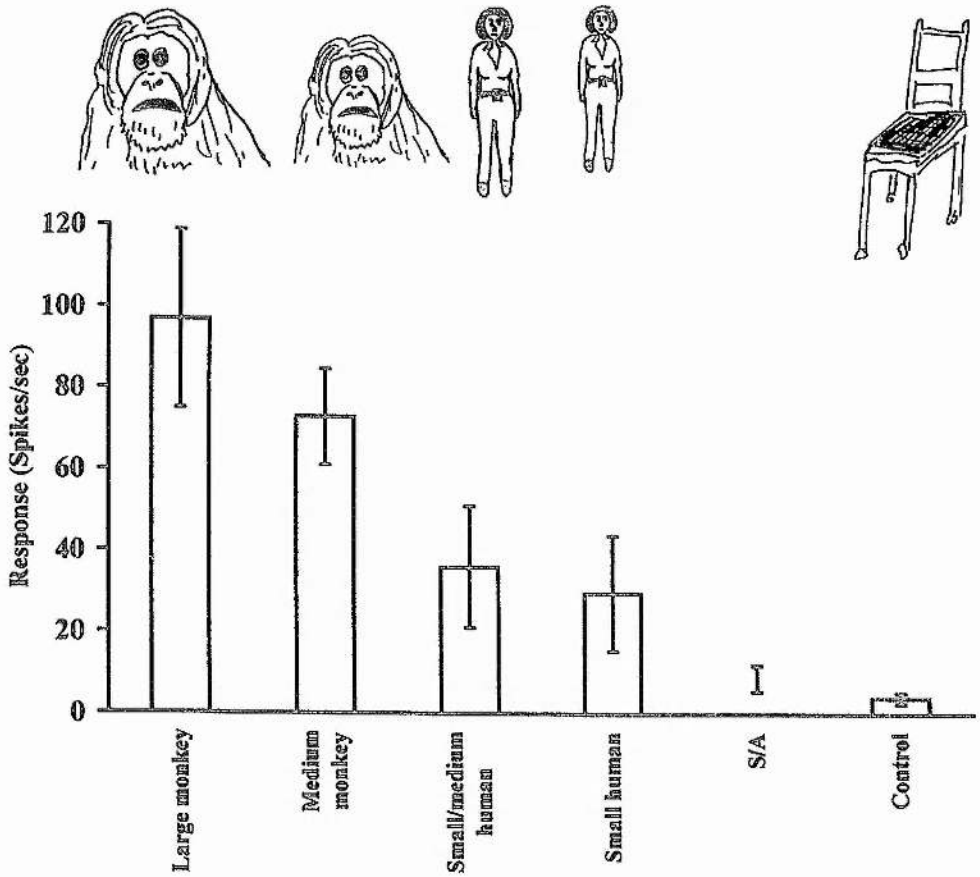


Figure 8.5. Neuronal responses of a cell responsive to large monkey figures compared to small human figures. Mean responses (+/- SEM, n=5 each category) to a large-sized 3D monkey figure, a medium-sized 3D monkey figure, a small-medium-sized 3D human figure, a small-sized 3D human figure, large, medium and small 3D control objects and S/A for one cell (E97_3988). There was a significant effect of condition, ANOVA: $F(5,24) = 7.62$, $p < 0.0001$, with responses to the large and medium-sized monkey figures significantly different from the small-medium-sized and small human figures, controls and S/A (PLSD, $p < 0.05$ all comparisons).



amygdala (see Chapter III), one of the functions of which may be to attach emotional significance to objects and events (Nishijo, Ono and Nishino 1988b, LeDoux 1996). The cell responsive to monkeys, humans and hawks may have been tuned to respond to low level features of faces, common to many vertebrates such as faces with forward facing eyes, with dark features (e.g. hair/feathers on the face, not skin).

One cell was significantly more responsive to the presentation of humans compared to monkeys. The cell was tested for two views (0^0, 180^0) of monkeys and humans. The cell's response was sensitive to human view 180^0 compared to monkeys (both views) and human view 0^0 (PLSD, $p < 0.05$, all comparisons) and significantly greater than controls and S/A (PLSD, $p < 0.05$). The responses of this cell are displayed as histograms in Figure 8.6.

Cells with responses which are sensitive to the differences between monkey and human faces (i.e. cells which are more responsive to one species over another), may be responding to features which differ between human and monkey faces. The cells may, however, be components of a system coding for human faces as a fraction of a larger category coding for primates' faces. More than two species of macaques, for example, were not tested for differential influences on cell response. The results of behavioural experiments described in the introduction suggested that macaques have a preference for rhesus macaques and closely related species. This ultimately suggests that macaques can process the differences between closely related species from visual cues. Further studies of cells must test multiple closely related species to determine whether single cells in the STS have the capacity to differentiate between different species of non-human primates.

One cell was equally responsive to a human and a monkey when compared with other species, different objects (jumbled human face, infant rhesus monkey, seal, toad, stumptailed macaque perineal region, room view, random dots, a syringe) and S/A. The cell was responsive to a human (whole body) and a rhesus monkey head (PLSD, $p < 0.05$ all comparisons). The response of this cell are displayed as a histogram in Figure 8.7.

The results presented above suggest that cells responsive to human faces are also responsive to other animal species. Some cells respond greater to humans, some to monkeys, some to monkeys and humans and some to a number of different species. The

Figure 8.6. Neuronal responses of a cell sensitive for one view of a human head and body compared to two views of a monkey head and body. Mean responses (+/- SEM, n=5 each category) to two views (0^0, 180^0) of human and monkey's whole bodies, control objects and S/A for one cell (S18_2285). There was a significant effect of condition, ANOVA: $F(5,24) = 4.27$, $p < 0.01$. The cell response was selective for human view 180^0 compared to monkeys (views 0^0 and 180^0) and human view 0^0, controls and S/A (PLSD, $p < 0.05$, all comparisons).

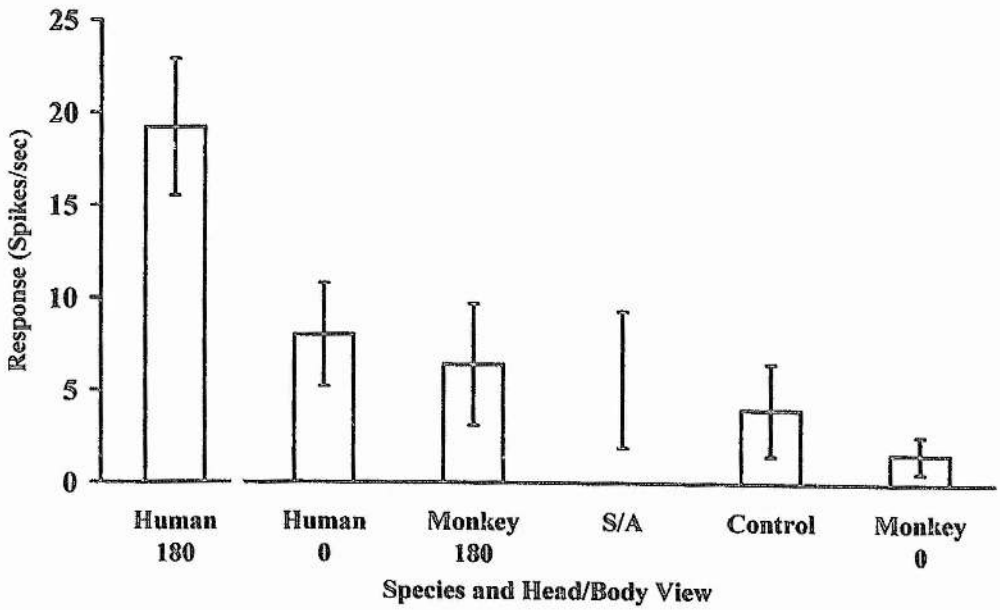
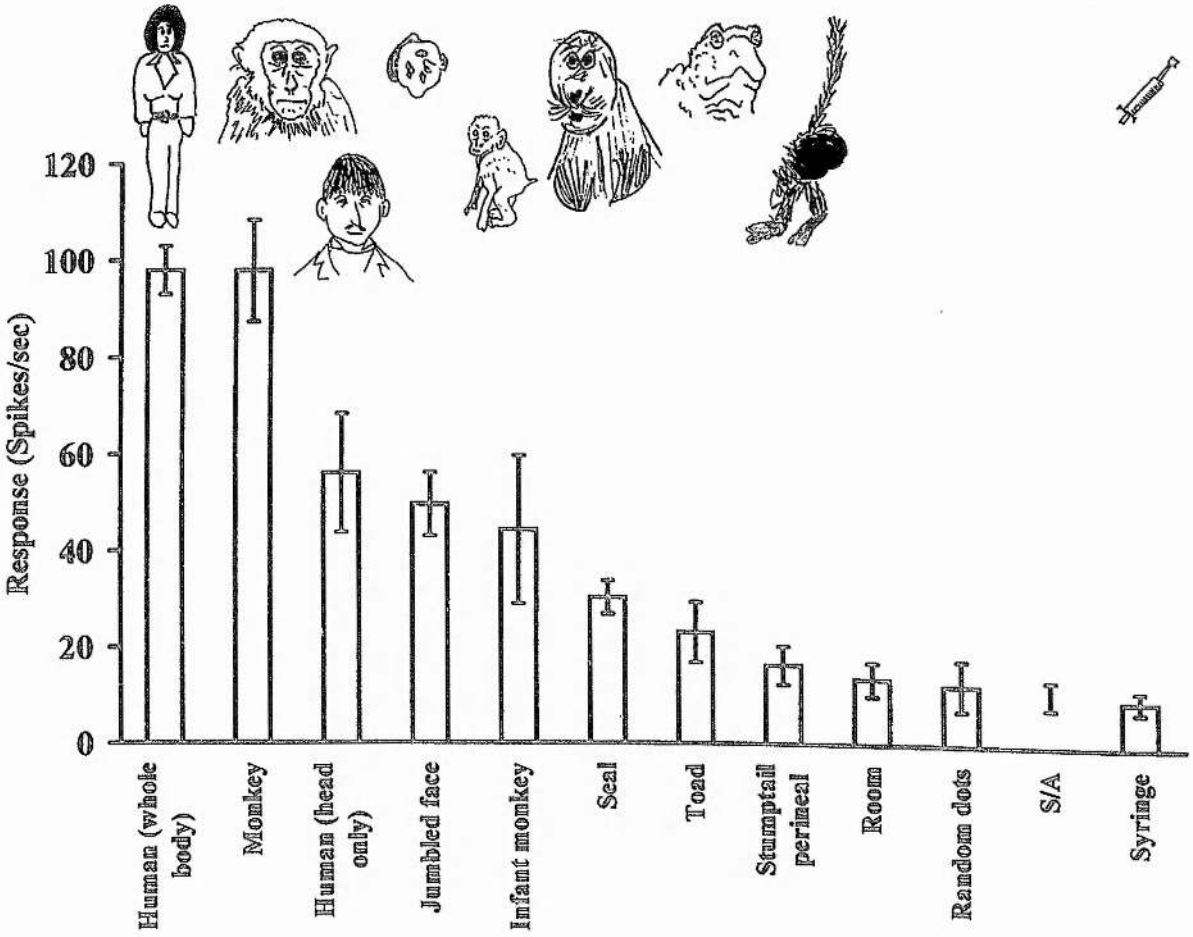


Figure 8.7. Neuronal responses of a cell responsive for human and monkey faces. Mean responses (+/- SEM, n=5 each category) to a human (head only and whole body, view 0^0), an adult rhesus macaque (whole view 0^0), an infant stumptailed monkey, a jumbled human face, a seal, a toad, stumptailed macaque perineal region, a room view, a random dot pattern, a syringe and S/A for one cell (E83_3831). There was a significant effect of condition, ANOVA: $F(11,48) = 17.88$, $p < 0.0001$. The responses to the human whole body and adult rhesus macaque were significantly different from all other species, control objects and S/A (PLSD, $p < 0.05$ all comparisons).



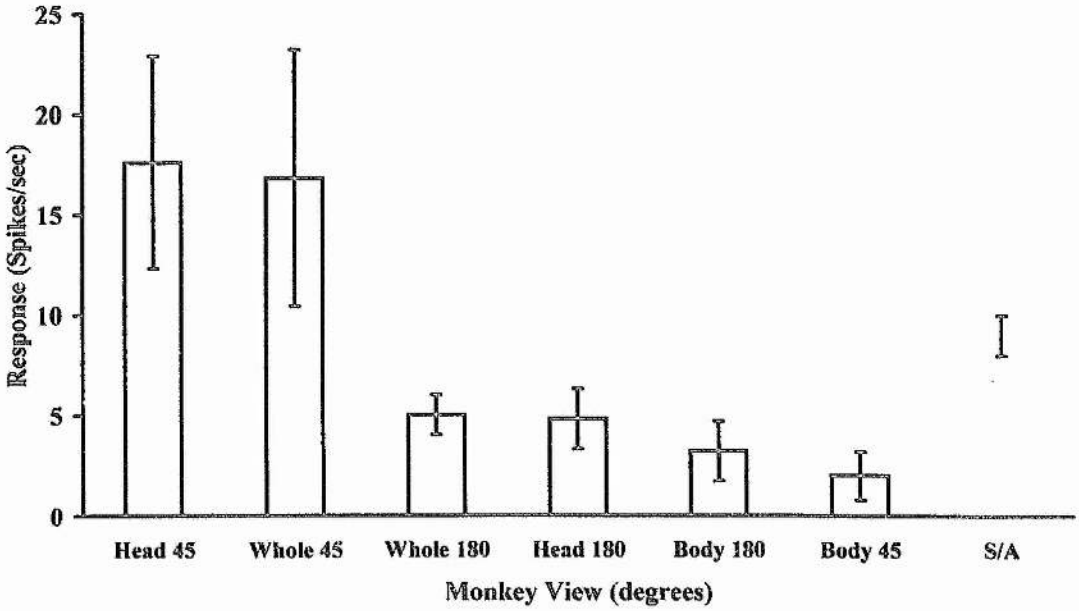
sensitivity of the cells tested does not appear to cluster around particular species. The cells reported in this section may code for species' faces as a population rather than coding for monkey face only or human face only. Primate faces are basically similar in appearance, particularly between closely related species (for example bonobos and chimpanzees have very similar faces, but humans and lemurs have similar features, but dissimilar faces).

To date, a number of physiological studies have tested differential responses to human and monkey faces (Desimone et al 1984, Perrett et al 1984, Rolls 1984, Baylis and Rolls 1987). The differences between responses to different species may be as great as between different individual human faces (Perrett et al 1994, 1987, Hasselmo et al 1989, Young and Yamane 1992, 1993). Young and Yamane (1993), for example, report that some cells (in AIT and STP) reponded to a small subset of human faces, whereas the response of one cell (in AIT) was narrowly tuned to the presentation of one particular human face (when tested with 27 different human faces).

2. Monkey body parts

Chapter VII reported that a number of neurons within the STS were responsive to human head and body view specificity. Other neurons with responses to front views of the human head, were sensitive to the position of the eyes. The previous section suggested that cells within the STS may either be equally responsive or more reseponsive to monkey faces than human faces (and bodies). Overall, five cells with responses to human body parts, were tested for sensitivity to monkey body parts. Two cells were tested for multiple views of monkey body parts. One cell was tested for view (45^0, 180^0) of different body parts (head only, body only and/or the whole body). The cell was selectively responsive to rhesus monkey head and whole body (classified as a cell responsive to the head, see Wachsmuth 1995) when oriented to present a half-profile view (45^0 from the face). The responses to the head and whole body (view 45^0) were significantly different from all body parts, view 180^0, body only, view 45^0, control objects and S/A (PLSD, $p < 0.05$, all comparisons). The responses of this cell are displayed as a histogram in Figure 8.8.

Figure 8.8. Neuronal responses of a cell sensitive for monkey head (view 45^0). Mean responses (+/- SEM, n=5 each category) to two views (45^0, 180^0) of rhesus monkey body parts (head only, body only, whole body), and S/A for one cell (E82_3799). There was a significant effect of condition, ANOVA: $F(7,28) = 3.28$, $p < 0.05$. The responses to the head only and whole body (both view 45^0) were significantly different from body only (view 45^0), head only, body only and whole body (all view 180^0) and S/A (PLSD, $p < 0.05$, all comparisons).



Two cells were tested for sensitivity to monkey body parts directed towards one view. One cell was more responsive to a rhesus monkey head and whole body, view 90^0 than to body only, view 90^0, control objects and S/A (PLSD, $p < 0.05$, all comparisons). The responses of this cell are displayed as a histogram in Figure 8.9a. A second cell was more responsive to a rhesus monkey head and whole body, view 0^0, than to body only, view 0^0, control objects and S/A (PLSD, $p < 0.05$, all comparisons). The responses of this cell are displayed as a histogram in Figure 8.9b.

A further cell (E84_3850) was responsive to multiple views of a rhesus monkey head and whole body (views 0^0 and 180^0), ANOVA: $F(4,33)=5.14$, $p < 0.01$. There was no difference in response between the two views (PLSD, $p > 0.05$). The response to the whole body was greater than to the body alone, controls and S/A (PLSD, $p < 0.05$, all comparisons), but not greater than the response to the head alone (PLSD, $p > 0.05$).

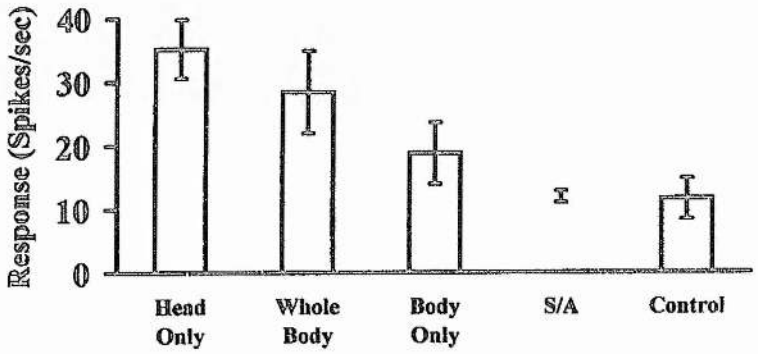
One cell was tested with multiple body parts (head only, body only, whole body, top of the head, head with eyes closed, hand and tail). The images were taken from the same species, but from different individuals. The head only stimulus was larger than the head on the whole body slide. The response to the head, view 0^0 was significantly greater than to all other body parts, control objects and S/A (PLSD, $p < 0.05$, all comparisons). It is possible that the cell was responding to the size of the head, however as there was a drammatic reduction in response with the presentation of the monkey face with the eyes closed. A histogram displaying the responses of this cell is presented in Figure 8.10.

The responses of the first three cells were view tuned and the responses could be attributed to visual features of the head. The presence of the head was necessary and sufficient to evoke responses. By contrast the body was not necessary or sufficient to evoke responses. Wachsmuth et al (1994) and Wachsmuth (1995) reported that a number of cells within the STS were responsive to the presentation of human body parts (head only, body only or the whole body). It is not surprising that neurons within the same area of cortex are also responsive to monkey body parts.

Fujita (1993b) suggested that pig-tail macaques made preferences for species, based on combinations of body features (including the head), not just single features. The majority of cells reported in this section required the presence of the head, but not the

Figure 8.9. (a) Neuronal responses of a cell sensitive for monkey whole body (view 90^0). Mean responses (+/- SEM, n=5 each category) to rhesus monkey head only, body only and whole body (view 90^0), control objects and S/A for one cell (E90_3500). There was a significant effect of condition, ANOVA: $F(4,20) = 5.5$, $p < 0.01$. The responses to head only and whole body were significantly different from controls and S/A (PLSD, $p < 0.05$, all comparisons). The response to head only was significantly different from body only (PLSD, $p < 0.05$), but the difference between whole body and body only was not significant (PLSD, $p > 0.05$). **(b) Neuronal responses of a cell sensitive for monkey whole body (view 0^0).** Mean responses (+/- SEM, n=5 each category) to rhesus monkey head only, body only and whole body (view 0^0), control objects and S/A for one cell (E99_4016). There was a significant effect of condition, ANOVA: $F(4,20) = 5.16$, $p < 0.01$. The responses to monkey whole body and head only were significantly different to controls and S/A (PLSD, $p < 0.05$, all comparisons). The response to body only was significantly different to control objects (PLSD, $p < 0.05$), but not significantly different from S/A (PLSD, $p > 0.05$).

(a)



(b)

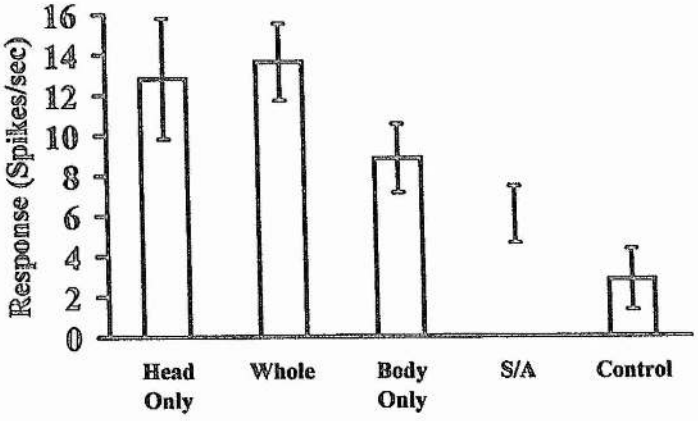
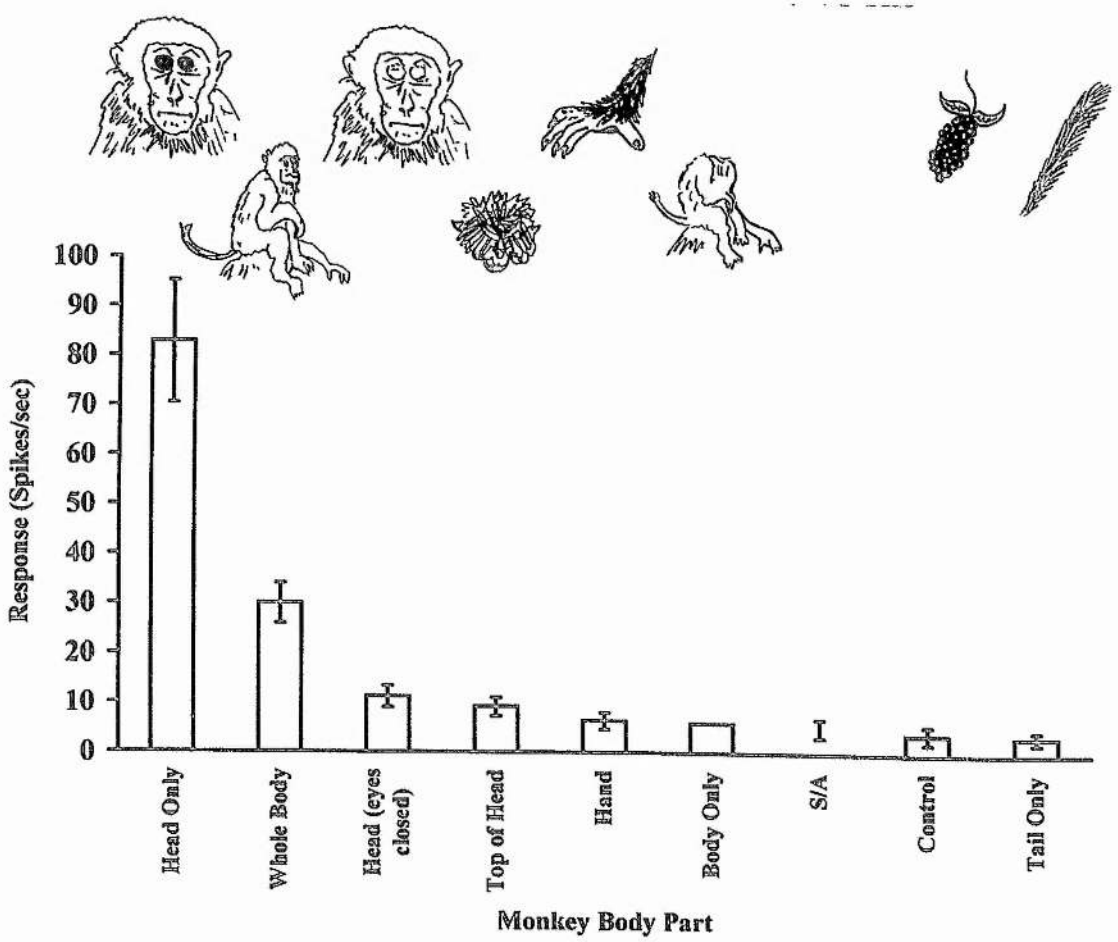


Figure 8.10. Neuronal responses of a cell sensitive for monkey head, compared to other monkey body parts. Mean responses (+/- SEM, n=5 each category) to monkey multiple body parts (head only, body only, whole body, top of the head, head with eyes closed, hand and tail, control objects and S/A for one cell (E80_3700). There was a significant effect of condition, ANOVA: $F(8,36) = 31.5$, $p < 0.0001$. The cell response to the head was significantly different to all other body parts, controls and S/A (PLSD, $p < 0.05$ all comparisons).



body presented without the head. One cell was responsive to the head alone compared to a number of body parts, but the cell may have differentiated between body parts on size alone. It is unlikely that the body suppresses information from the head (as would be suggested by a maximal response to the head, but a reduced response to the whole body, which includes the head). Dittrich (1994) suggested that a monkey's ability to recognise another species was only dependent on the presence of the torso (not requiring the presence of the head or the extremities). This suggestion appears to be at odds with the data presented here and Wachsmuth (1995) and the behavioural results of Fujita (1993b) which all emphasised the importance of the head in recognition. Differences in stimuli, may account for the differences in results. Dittrich (1994) used black and white line drawings of profiled whole bodies as stimuli, whereas Fujita (1993b), this study and Wachsmuth (1995) all used clear, colour, photographic stimuli.

3. Monkey eye gaze

The responses of two cells were dependent on the position of the eyes in a monkey head, view 0^0. The responses of one cell were found to be sensitive to the eyes averted (right, left or up), with responses greater than when the eyes were facing the viewer (ahead), control objects and S/A (PLSD, $p < 0.05$, all comparisons). Responses to eyes right and eyes left were significantly different from responses to eyes up, eyes down (i.e. partially occluded), eyes ahead (PLSD, $p < 0.05$, all comparisons). Responses to eyes up were significantly different from eyes ahead, controls and S/A (PLSD, $p < 0.05$, all comparisons). A histogram displaying the responses of this cell are presented in Figure 8.11.

The second cell was also responsive when the eyes were averted from the viewer in a monkey head, view 0^0, compared to the eyes ahead. The responses to the eyes right and eyes left were significantly different from eyes ahead, eyes down, eyes up, controls and S/A (PLSD, $p < 0.05$, all comparisons). The responses of this cell are displayed as a histogram in Figure 8.12.

Figure 8.11. Neuronal responses of a cell selective for a monkey with the eyes averted. Mean responses (+/- SEM, n=5 each category) to monkey head view 0^0, with different eye positions relative to the viewer (eyes right, eyes left, eyes up, eyes down and eyes facing the viewer), control objects and S/A for one cell (E82_3700). There was a significant effect of condition, ANOVA: $F(6,28) = 9.52$, $p < 0.0001$. The responses to eyes right, eyes left and eyes up were significantly different from eyes down, eyes facing the viewer, controls and S/A (PLSD, $p < 0.05$ all comparisons).

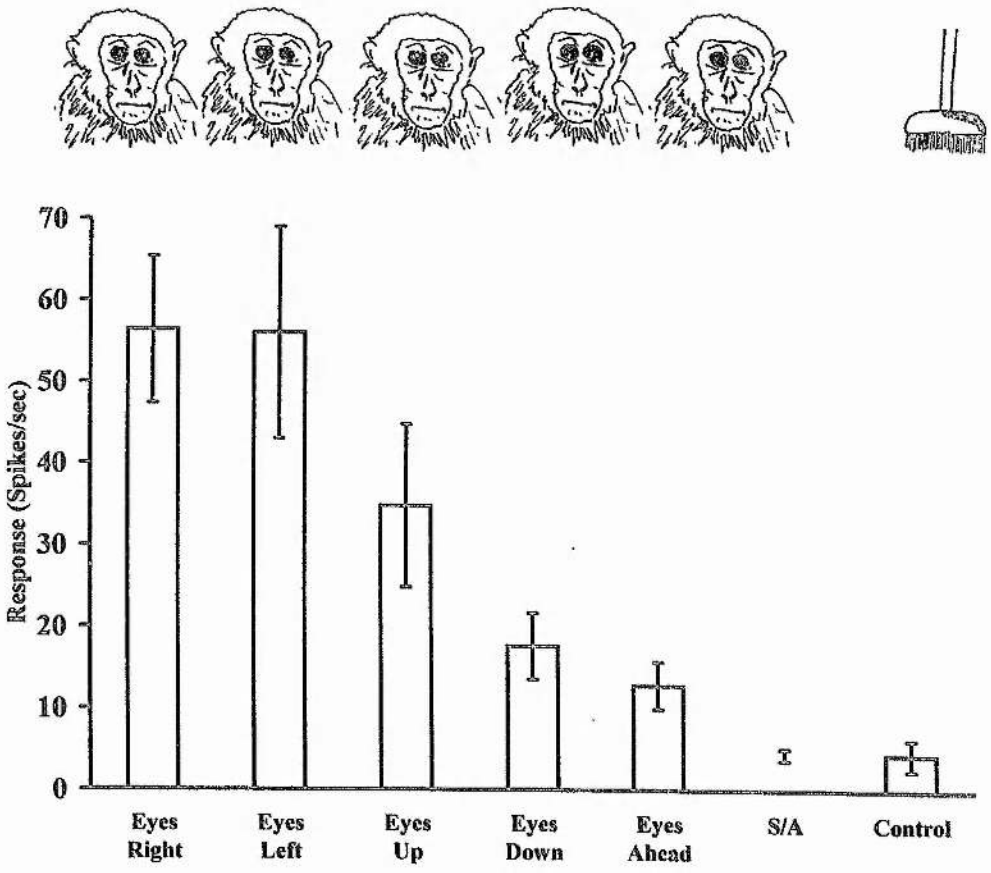
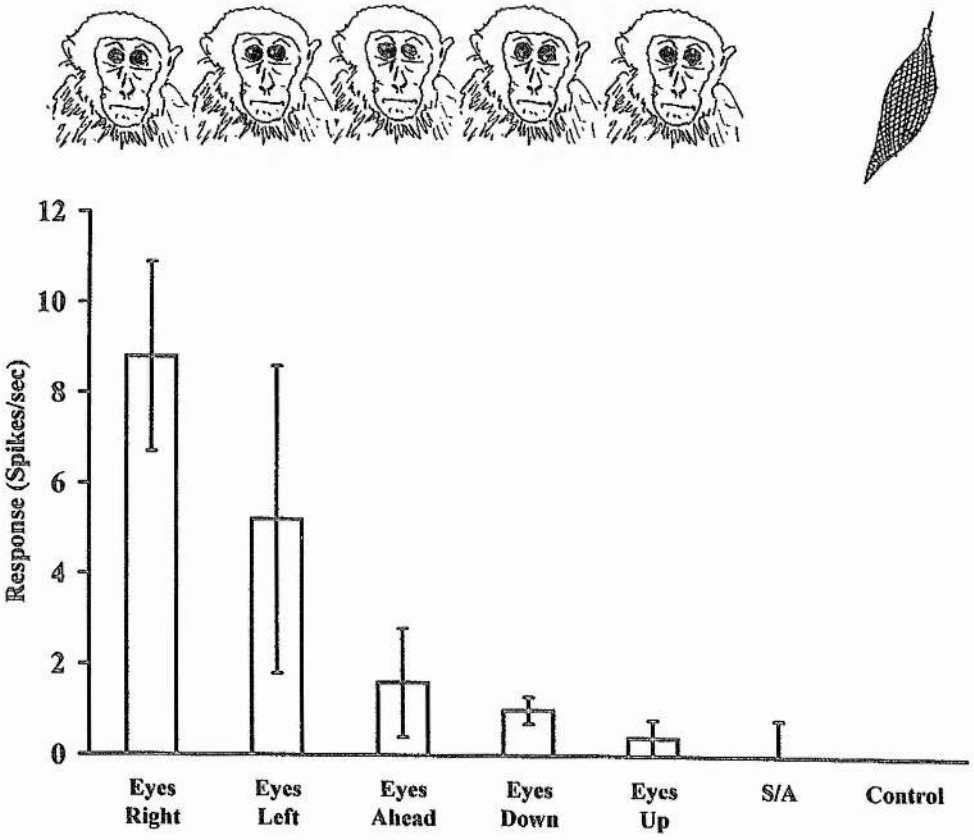


Figure 8.12. Neuronal responses of a cell selective for monkey eyes, horizontally averted. Mean responses (+/_ SEM, n=5 each category) to monkey head view 0^0, with different eye positions relative to the viewer (eyes right, eyes left, eyes up, eyes down and eyes facing the viewer), control objects and S/A for one cell (E81_3609). There was a significant effect of condition, ANOVA: $F(6,28) = 4.07$, $p < 0.01$. The cell responses to eyes right were significantly different from eyes facing the viewer, eyes down, eyes up, control objects and S/A (PLSD, $p < 0.05$, all comparisons). There was no difference between the responses to eyes right and eyes left (PLSD, $p < 0.05$). The response to eyes left was not significantly different to eyes facing the view or eyes down, but was significantly different to eyes up, controls and S/A (PLSD, $p < 0.05$).



Eye gaze is as important a means of social communication in monkeys and apes, as it is in humans (see Chapters VII and IX for reviews). Rhesus monkeys interpret direct gaze as a threat, and averted gaze as a submissive gesture (Redican 1975). Stimuli consisting of monkey faces with different eye positions would be expected to elicit cell responses as strong or stronger than those seen after presentation of similar human stimuli. The response of the cells described in this section were both responsive to the sight of monkey faces (view 0^0) with eyes averted from the observer. The cells may therefore be responding to submissive, rather than threatening gestures. Again, this may a component of coding an emotional response (possibly conducted by the amygdala).

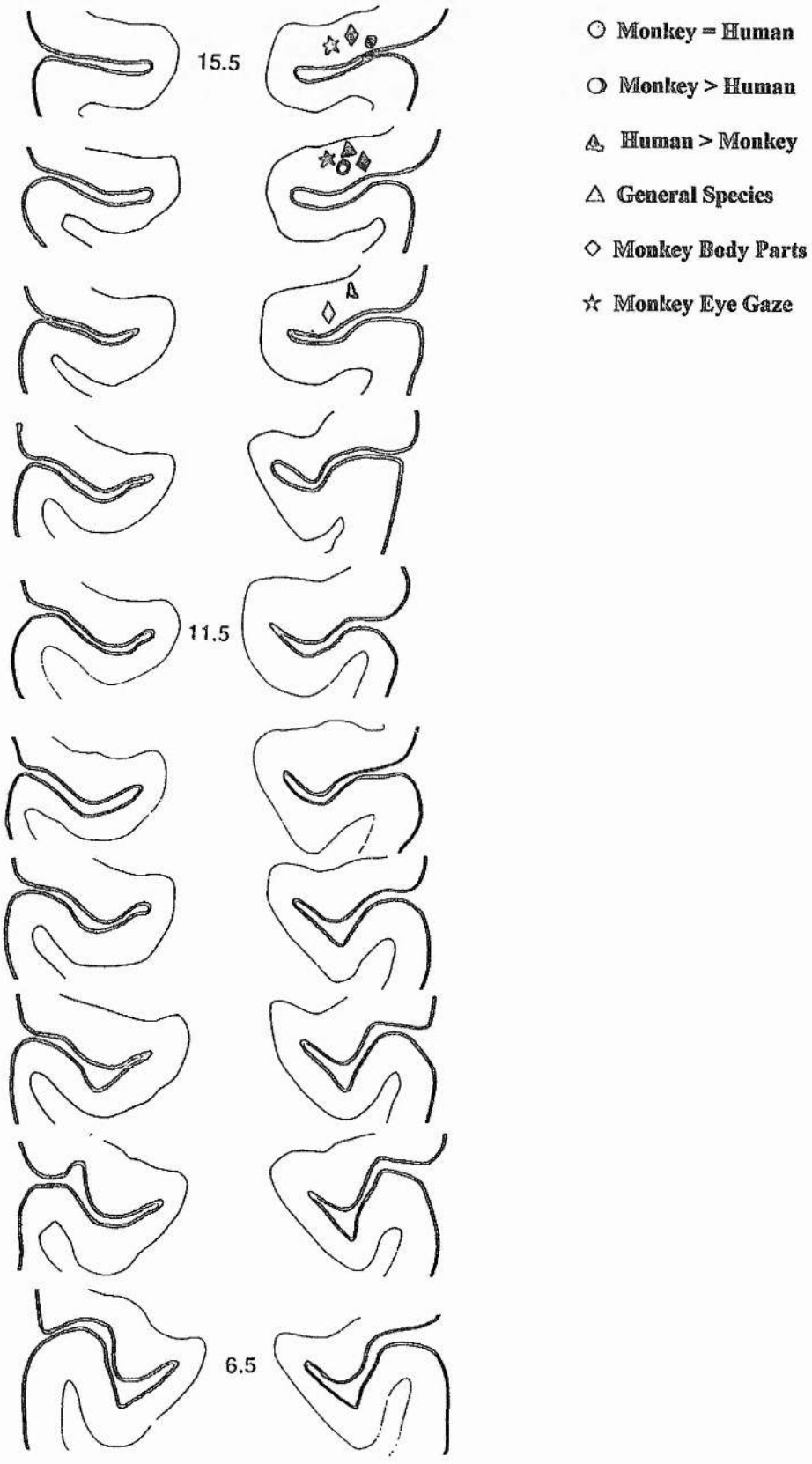
8.3.3 Histological reconstruction

Histological data is not available from subject Steve as this monkey is still being used in ongoing neurophysiological and behavioural experiments. The reconstruction of cell postions within subject Esther (see Chapter VI for methods), indicated that cells responsive to the stimuli discussed in this chapter were located in the upper and lower banks of the anterior STS (see Figure 8.13).

8.4 General Discussion

It is difficult to make assumptions about the function of a brain region from the results of a small number of cells. A large number of studies have established that one of the functions of the superior temporal sulcus is to recognise faces as a distinct class of objects, which have functional importance in social behaviour and communication of social signals. The physiological studies described in the introduction and in the results section of this chapter, provide some evidence that the responses of a number of neurons in the STS are not only specific for the sight of faces, but also sensitive to different species' faces. Behavioural studies suggest that monkeys can differentiate between the sight of different species (and individuals within the same species). The responses of the

Figure 8.13. Histological reconstruction: Species. Series of frontal sections of the STS every 1mm (6.5 {bottom} to 15.5mm {top} anterior to the interaural plane) reconstructed from one monkey (E) showing the location of cells responsive to monkeys = humans (filled circles), monkeys > humans (open circles), humans > monkeys (open triangles), general species (filled triangles), monkey body parts (filled diamonds) and monkey eye gaze (stars).



cells reported here may be pooled together to aid the recognition of sub-categories of different animal faces within a larger category of faces.

The question arises, why would it be adaptive for the primate brain to contain specific neural systems which respond to the sight of conspecifics? Conspecifics are likely to produce or react to species-typical behaviours (including social signals) than non-conspecifics and therefore are more likely to take part in social interactions. There is a large benefit of the brain containing dedicated neural subsystems which process the visual appearance of conspecifics versus other animals.

There are a number of possible reasons why the monkey brain contains cells which are responsive to the sight of both humans and monkeys. First, the cells may be responding to a large category (e.g. faces). This proposition only explains the responses of neurons to presentations of different species' faces. It does not explain the responses of cells described above or in earlier studies, which were biased to respond to one species' face (monkeys > humans or humans > monkeys). Second, the cells may be responding to a smaller category of faces (e.g. primates), to which monkeys and humans belong. The responses of these cells may be processed earlier than the responses of category specific cells (e.g. cells which respond only to the sight of monkeys or humans). Finally, laboratory primates may gain equal (or almost equal) benefits from caregiving humans (food and drink) and from other monkeys (social interaction, play, sex, etc.). Cells responsive to the sight of monkey and human faces may equate to the salience and benefits provided by humans and other monkeys.

Cells which respond to monkeys, humans and other animals may be responding to specific categories such as animal faces, facial components (eyes, mouths, noses) or a general category of animate objects, which include faces. A number of studies suggest that the human and non-human primate brain may contain domain-specific regions which code for knowledge of animate and inanimate objects.

Farah, McMullen and Meyer (1991) studied two patients with visual agnosia and tested the patients' knowledge of living and non-living things. Some authors (e.g. Damasio 1990) have suggested that difficulties in processing living things are due to the similarity of visual features of living things (see also Gaffan and Heywood 1993). A

second suggestion is that non-living things have a function and that recognition is enhanced by visualising the use of the object as well as the visual organisation of the object. For example, a pair of scissors can be visualised as an object with two blades, but recognition may be enhanced by visualising the cutting action of the scissors. Farah et al. found that the deficit in processing living things was still present after using multiple regression analysis to partial out the effects of similarity, visual complexity, familiarity and function. This effect was replicated by Farah, Meyer and McMullen (1996) using multiple presentations of the same object. Funnell and Sheridan (1992) found that the living/non-living distinction was removed when single presentations of the same object were introduced to the subjects. Farah et al suggested that the results were not due to a deficit in category-specific processing (living versus non-living), but a deficit in modality-specific coding of objects (see also Gaffan and Heywood 1993).

Gaffan and Heywood (1993) used normal human and monkey subjects to test the hypothesis that processing differences between living and non-living objects, were due to the similarity between living things (i.e. all have legs, a face, a body). This was also counter to previous arguments that all living things are classified together in a large category of animate objects. Gaffan and Heywood found that there was an increase in the number of errors made by human subjects during recognition of living things (versus recognition of non-living things). (The stimuli were only presented for 20 ms and in low contrast, to produce a high number of errors.) A similar result was obtained with normal rhesus monkey subjects. The monkeys were trained to make a choice between a picture of a living versus a non-living thing, with reward. When the number of pictures to discriminate was increased from the number presented in training, the dissociation between living and non-living was clear. More errors were made for discriminating living things.

Gaffan and Heywood suggested that "category-specific impairment of knowledge of living things in patients with visual agnosia can ..be explained as arising directly from the visual similarity to each other as members of a visually crowded category" (1993, p. 126).

The data presented in this chapter suggests that two mechanisms of coding faces may be working in the monkey brain. Cells coding for all species (i.e. living things) or monkeys AND humans (i.e. primates) may not be coding for category, but the visual similarity between species faces (two eyes, a nose, a mouth, etc.). These cells may be low-level feature detectors and may respond earlier than more complex feature detectors. Cells coding for the sight of either monkeys only or humans only may be category-specific, as the gross features are similar, but the functional properties of the face are different (i.e. monkey = social interaction, human = fear). A third system may code for the recognition of inanimate objects (such as food, tools), such as many of the control objects presented in tests. Coding for the sight of geometrical features and complex objects, which may form parts of inanimate (such as tools) and animate objects (such as faces) occurs mainly within the inferotemporal cortex (Tanaka et al 1990, Tanaka 1993). Some neurons responsive to the sight of different foods have been reported in the orbitofrontal cortex (Thorpe et al 1983), amygdala (Ono et al 1983, 1989) and lateral hypothalamus (Rolls, Burton and Mora 1976, Ono et al 1989) .

Recent evidence suggests that different neural systems code for the differences between animate and inanimate objects. Martin et al (1996) tested normal subjects in a PET scanner, whilst the subjects viewed pictures of animals and tools. Effects of naming aloud were removed by making one half of the subjects name the objects loudly and the other subjects name the objects silently. Martin et al concluded that naming biological objects requires basic recognition (possibly also how an animal moves). Naming tools requires processing the function and action of that tool. Martin et al. Found that there was a neural dissociation between naming the two categories of objects. Naming animals was associated with bilateral activation of the ventral temporal lobes (parahippocampal gyrus, fusiform gyrus) and the left medial occipital lobe. Tool naming was also associated with bilateral activation of the ventral temporal lobes, the middle temporal gyrus and the left premotor cortex (A6).

Activity in the premotor cortex corresponds with PET studies in human subjects, where subjects imagined grasping objects and this was associated with a significant activation in the premotor area (Decety et al 1994). Activation of the ventral temporal

lobes with the presentation of animal stimuli (Martin et al 1996) may relate to studies of neurons within the macaque ventral temporal cortex (STS) which respond to bodies walking (Perrett et al 1985a, Oram and Perrett 1996, see Chapter VII). The response of cells in the anterior STS to monkeys and humans walking quadrupedally, bipedally and while crouched down have been tested, with some cells sensitive to each type of motion (Perrett et al 1984). The response of cells responsive to walking bodies have not been tested with other types of animal motion which involve four limbs (such as a horse cantering, a cat pouncing or a rat scurrying). A prediction would be that these types of motion would elicit different responses to bipedal human walking. Recognition of animals in humans, may be dependent on imagining the method by which an animal moves.

As stated previously, it is impossible to make any concrete conclusions about the function of this brain area from the results of a small number of cells. Face-selective neurons have been found within a large number of brain areas (see Perrett et al 1992 for review of temporal cortex cells; amygdala, Rolls 1984; temporal pole, Nakamura et al 1994; prefrontal cortex, Wilson et al 1993). It is probable that each area (or sub-area) is performing a different function in which faces are important.

The results of chapter VII suggested that the function of other neurons within the monkey anterior temporal cortex may be to code for the sight of attention (where others are looking), action (what others are doing) and intention (how others are going to interact with objects). The function of these neurons may be dependent on inputs from the cells described above (as social interaction is impossible without recognising other protagonists in the interaction). This idea is discussed further in Chapter IX.

Chapter IX

Gaze Processing in Monkeys: A Behavioural Investigation

(a shortened version of this chapter, in press J. Comp. Psych.)

"Non-human primates may use visual signals not only to signal their intentions, but also to communicate about the direction, amount and quality of external objects"

Zeller (1987, p. 439)

9.0 Summary

Gaze direction provides an important source of social information for primates. A large body of evidence suggests that feral primates can follow gaze. Monkeys and apes can gain information about available food sources, social dominance and the location of predators from the attention direction of conspecifics (Chance 1967, Menzel and Halperin 1975, van Schaik et al. 1983, Whiten and Byrne 1988a). Behavioural studies show chimpanzees spontaneously follow human gaze direction. By contrast, macaque and capuchin monkeys are reported to fail or have difficulty learning to use human gaze as a discriminative cue. This chapter provides results of the spontaneous reactions (eye movements) of rhesus macaques to social attention cues of conspecifics. Two subjects were presented with videotaped images of a stimulus monkey with its attention directed to one of two identical objects. Analysis of their eye movements revealed that both subjects inspected the target (object or position attended by the stimulus monkey) more often than the distracter (non-attended object or position). These results provide the first

experimental evidence that rhesus monkeys spontaneously use the direction of attention cues of other monkeys to orient their own attention.

9.1 Introduction

9.1.2 Definitions of gaze behaviour

When describing visual behaviour, the terminology used to summarise such a seemingly simple action as seeing is unhelpful at the least. Problems arise when individual authors fail to define the nomenclature they have decided to incorporate in their own particular studies. Before outlining the background to this study, the terms to be used will described and in what context they will be used.

'Gaze following' can be defined as the ability of one individual (X) to follow the direction of gaze of a second individual (Y) to some position in space (Povinelli and Eddy 1996b, Perrett & Emery 1994, Baron-Cohen 1994). Note that such a definition does not require that the individuals X and Y look at the same object it requires only that they look in the same direction (Figure 9.1a).

The direction of another's attention can be signalled not only by eye direction but also by a variety of cues such as head direction, body posture and the orientation body parts (e.g. pointing). In most situations, however, a subject's direction of attention will coincide with the direction of their eye gaze. Gaze direction has therefore often been used as a shorthand for direction of attention. In many cases it remains to be determined which cues (eye direction, head posture etc.) are used by subjects when 'gaze' following. The term gaze following will refer to the use of any of the available sources of information (eyes, head, body and movement cues) when one individual redirects its own gaze direction to match the direction of attention of a second individual.

'Joint attention' can be defined in the same way as gaze following but with the additional requirement that X follows the direction of gaze of Y to the object (Z) that is the focus of Y's attention (Figure 9.1b). Note that this definition does not require mutual

attention between X and Y. X does not have to interact with Y to follow the direction of Y's attention.

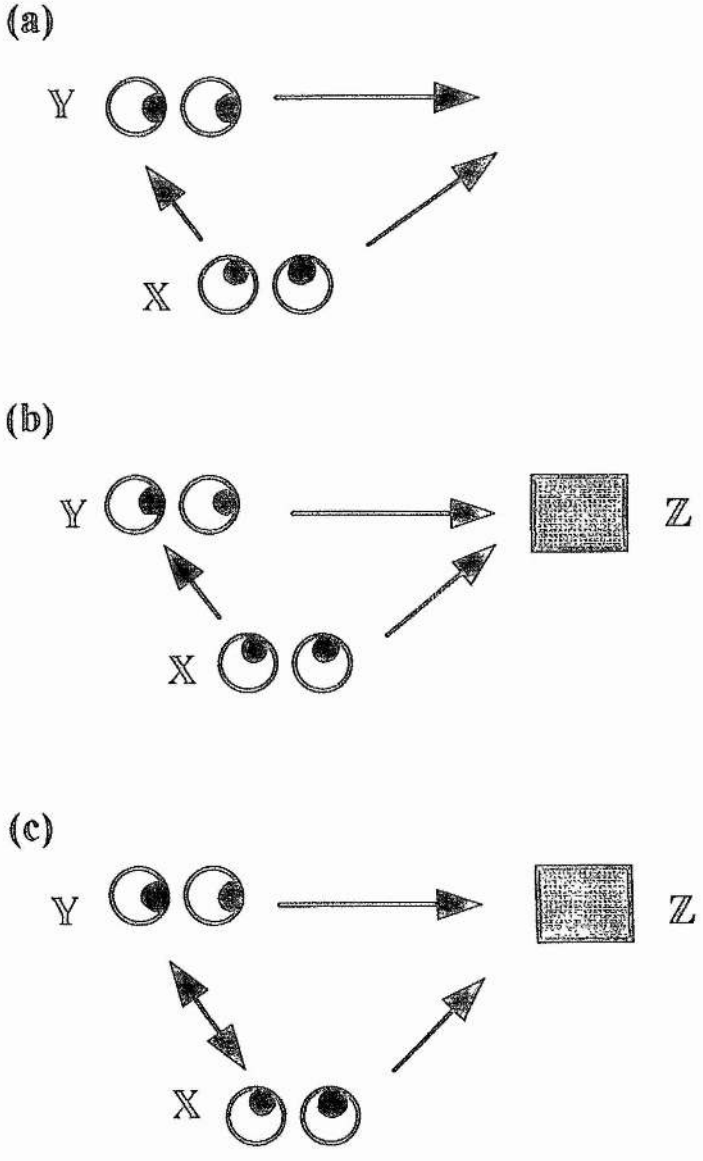
'Shared attention' can be defined as the ability of one individual to interact with a second individual and to follow the attention direction of the other's attention to an object. The concept of sharing requires a mutual awareness that both individuals are attending to the same object (see Figure 9.1c). One cannot infer from gaze monitoring that the individuals necessarily are sharing anything. The terms above have been used interchangeably in previous literature (Baron-Cohen 1994, 1995).

9.1.3 Evolution of gaze recognition

The eyes have long held special interest to humans; they are said to be the *window to the soul* (Baron-Cohen 1996), they are often used as symbols of a curse (*evil eye*) or as warning signals, but are also one of the first points of contact between newborn infants and their mothers (Haith, Bergman and Moore 1977). Non-human primates are also attracted to the eyes, and use their eyes for many communicative functions, such as warning others of their disposition (threatening or submissive). This small review discusses the attraction of the eyes to a number of animals focusing on how primates process information about the eyes, head and bodies of others and how information from body parts can be used in communication.

An important function of recognising the presence of eyes and eye-like stimuli is to determine whether they are looking at or away from you. A large number of species appear to perform this discrimination. Black iguanas (*Ctenosaurua similis*) appear to discriminate that an approaching human is looking towards or away from the iguanas (Burger et al. 1992). Burger et al suggested that iguanas associate gaze contact and direct approach as threatening and escape quicker than when the same experimenter is directly approaching, but looking away from them. Iguanas also appear to be sensitive to the size of the approaching eyes, by responding when the eyes are larger (Burger et al.1991).

Figure 9.1. Levels of social interaction using gaze. **(a)** Schematic representation of *gaze following* (dyadic relationship), where an Observer (X) follows the direction of gaze of the Observed individual (Y). **(b)** *Joint attention* behavior (triadic relationship) where an Observer (X) follows the gaze of the Observed (Y) onto an object (Z). **(c)** *Shared attention* behaviour (triadic relationship), where the above criteria for joint attention are present, but also the Observer (X) and Observed (Y) are mutually attending to each other so X and Y are shifting gaze between the object and the other individual (Perrett and Emery 1994).



Some species of bird can also perform this discrimination. Ristau (1991) studied plovers' (*Charadrius*) reactions to human experimenters who walked past their nests either looking at the plover's nests in the dunes, or in the opposite direction towards the ocean. Ristau determined that plovers incubating their young remained off the nest for longer under threatening situations. Plovers remained off the nests for longer when an experimenter was gazing towards the plover's nest than when the experimenter was gazing towards the sea.

Gallup, Cummings and Nash (1972) also looked at birds responsivity to human gaze. Chickens (*Gallus gallus*) respond to staring humans by becoming rigid (*tonic immobility)*. This is said to correlate highly with fear (Gallup et al 1972). The length of immobility was greatly reduced when the eyes of an experimenter were directed away from the chickens. The same phenomenon has also been reported in anoles (*Anolis carolinensis*), a species of lizard (Hennig 1977).

A related phenomenon to tonic immobility is *death feigning* (as seen in hog-nosed snakes). This occurs in reaction to eyes directed towards the snakes (Burghardt 1990). Whether these actions are innate behaviours or learnt through extensive experience with predators is not known and out of the scope of this review. Scaife (1976a, b) suggests that the ability to discriminate eyes as a stimulus which is part of the face, is an innate ability.

Other avian species have been tested for their responsivity to specific human head orientations and gaze directions. House sparrows (*Passer domesticus*) were found to increase flight responses (escape response) when a face was directed towards the birds, but the sparrows were unresponsive to the direction of the eyes, whether pointed away or toward the subjects (Hampton 1994). The sparrows, however, could determine the line of gaze from the number of eyes visible. This result has significant evolutionary consequences as most predators have two forward facing eyes, so when only one eye is visible, this signals to the prey that the predator's head is turned away, and that the predator's attention is elsewhere.

Primates possess a great interest in the eyes and the region around them. How primates *use* the information transmitted by the eyes will be discussed in the next

sections. Experimental laboratory studies of face recognition in monkeys have highlighted the interest some species of primate have in the eyes. Keating and Keating (1982) studied the eye movement responses of two rhesus monkeys while the subjects viewed different primate faces (rhesus monkey, chimpanzee and human) with neutral expressions, and also to schematic faces. The subjects showed an extreme bias of looking at the eyes and the small region surrounding the eyes compared with the nose and the mouth for all four neutral face stimuli regardless of species.

Laboratory studies have also shown that baboons appear to look at the eye region more than other parts of the face. Kyes and Candland (1987) had baboon subjects study slides of other baboon faces and parts of faces. Although the subjects looked longer at the slides of full (complete) faces, they also inspect pictures which contained eyes longer than slides containing just the nose, or the mouth, or the nose and mouth.

Colour performs an important function in highlighting the eye region of some primate species. Kingdon (1980) described fully the facial patterns and colourations of the different species of guenon (*Cercopithecus*, Old World monkey). For example, *C. mona* and *C. cephus cephus* have bright blue colouration around the eyes, but no colouration of the genital area (white instead of the bright red colour of the majority of Cercopithecines, Gautier and Gautier 1977). This may be interpreted as an increased importance of the face and eyes and therefore use in facial expressions during sexual or social signalling, or an attempt to further enhance the differentiation between the face and the genital region. *Cercopithecus neglectus* have a wide orange-coloured brow-ridge which highlights the position of the eyes (Kingdon 1980). Species of guenon which do not have brightly coloured facial features, usually have brightly coloured genitals. It is interesting to note that the brightly coloured genitals are blue, and that the colour around the eyes of those species without the genital colouration is blue.

In all descriptions of primate facial expressions, the eyes play a pivotal role (Andrews 1963, 1964, Jolly 1972, Redican 1975, Bertrand 1969). Any discussion of the role of the eyes in primate emotional communication must mention the role of the whole face. The eyes are not processed separately from the rest of the face, they are analysed in concert with the other features of the face such as the nose, and mouth, and in particular

the ocular muscles surrounding and controlling the movements of the eyes. This is not to say that the eyes are not powerful tools in the expression of emotion alone. In some primates the effect of a stare without the accompanying facial movements is very effective in eliciting fear responses from conspecifics.

The majority of primates have very darkened eyes compared to humans. Kobayashi and Kohshima (1997) found that of eighty-eight primate species, only humans had eyes with a white sclera and a dark iris. The sclera of most primate's eyes was found to be brown, with two species (Old World macaques) having a pale brown sclera and four species (Old and New World monkeys) having a partly white sclera. The sclera of macaque infants is less pigmented than adults. Perrett and Mistlin (1990) discussed the reason why the sclera of adult macaques may become darker compared to infants. One possible function of the large dark iris/pupil may be for deceptive or protective purposes. Determining the precise direction of another's attention is difficult to assess when there is no differentiation between the sclera and the iris. In humans, interpreting gaze direction is made easier by the morphology of the eyes. Gaze following can be performed using a simple rule (dark in the centre of the eye equals eye contact; dark to the left of the eye equals looking left; dark to the right of the eye equals looking right). Perrett and Mistlin (1990) suggested that because the iris and sclera of non-human primates was dark, the monkeys could look out of the corner of their eye without invoking threatening gestures usually associated with eye contact from conspecifics.

Kaplan and Rogers (1996) discussed a similar behaviour in re-habilitant orangutans. Orangutans rarely look directly into the eyes of conspecifics. It is usual to see orangutans point their heads away from conspecifics, but with the eyes towards other individuals.

Primates have excellent discriminative abilities for determining whether they are being looked at or whether another's gaze is directed away from them. Keating and Keating (1982) studied two monkey subjects' eye movements in response to viewing slides of rhesus monkey gesturing faces. The expressive stimuli included a slide of a threatening rhesus face with a direct stare, a slide of a rhesus grinning with direct gaze, a slide of a rhesus with a neutral expression with direct gaze and a slide of a rhesus

submissive face with averted gaze. Both subjects looked at the eye region more often than the nose and mouth and looked at the faces with direct gaze (irrespective of facial expression) more than the face with averted gaze. This pattern was repeated when the subjects were presented with slides of human faces. Only slides of two human gestures were presented to the subjects, raised eyebrows and lowered eyebrows. The eye region elicited a higher number of fixations than the nose and mouth regions, but there were a higher number of fixations on the human faces with raised eyebrows.

Perrett and Mistlin (1990) reported the number of submissive gestures (lip-smacking and teeth-chattering) given in response to the presentation of either a head horizontally oriented towards the viewer or away from the viewer. The largest number of submissive gestures were made by the subjects independent of the position of the head, when the eyes were in contact with the observing monkey. This experiment was repeated for elevation of the head (Mistlin 1988). The raised head received less appeasement (submissive) gestures compared to a normal, level head position or a head averted laterally by 45 degrees. This was also found when Mistlin (1988) tested the emotional reactions of stumptailed monkeys to a life-sized model of a dominant male stumptailed macaque. The model's head and eyes could be positioned to give any head and eyes orientation or elevation combination. The lowered head received more appeasement gestures compared to the head raised or level.

A recent study of stump-tailed macaques has proposed another function for eye contact between male and females (Linnankoski et al 1993). Presenting females to single males caused the males to masturbate and ejaculate, but only when eye contact was established between the male and female. Other visual or olfactory cues such as inspecting the females perineal region were not as effective initiators of ejaculation as eye contact.

Physiological measures in non-human primates accompany the detection of eye contact. Wada (1961) studied the EEG responses from the brainstem of macaques to electrical stimulation of the cortex. He found that if he looked at the monkey subjects the EEG trace would change dramatically.

"When the animal discovered it was being watched, the response was depressed as long as the animal could see the experimenter....Such flattening regularly occured whenever the animal realized that the experimenter's gaze was fixed on it....the direct meaning of the experimenter's gaze...suggests concentrated focusing of discriminatory attention of a quality necessary for self-preservation"

Wada (1961, p. 41)

Although monkeys (Old and New world) do not appear to make distinctions between direct staring and mutual eye contact, the case would seem to be different for humans and great apes. Direct staring is different from mutual gaze or eye contact in a number of ways. Staring involves the eyes but also the eyebrows and brow ridges being raised to increase the visibility of the eyes, the ears being pulled back and the hair on the head standing up. Face-to-face sex is an example of the way that great apes such as bonobos (de Waal 1982), orangutans (Galdikas 1996) and humans (Morris 1967) may use looking into each other's eyes as a method for confirming and strengthening the sexual and affiliative bond (de Waal 1989).

It can, therefore, be concluded that primates (and other animals) class eyes as a separate class of objects, that direction of the eyes can be discriminated relatively easily by primates and that communication using the eyes maybe independent on head view. The next sections review evidence that primates can follow gaze (head and eyes in a specific direction) or body postures (such as pointing) to objects in the environment.

9.1.4 Gaze following and joint attention

Determining the precise direction of another's attention or *social attention* is an extremely important ability for non-human primates. Gaze provides salient cues about the location of objects, but may also function in complex forms of social cognition, such as visual perspective-taking, deception, empathy and theory of mind (see Chapter VII and Whiten 1996b, 1997a, b).

An important use for gaze following is in determining the position of an individual in a dominance hierarchy. Chance (1967) called this *social attention*, where "each individual [*in a social group*] accords and receives attention as a function of his or her

rank". The most dominant animal in a social hierarchy receives the highest number of glances (attention from less dominant animals), and glances at other animals the least. Chance states that members of a social group must have the capacity to determine 1) that the dominant individual is the focus of the others attention, 2) that these glances total more than those directed towards less dominant animals, and 3) that the group members extrapolate the information that the animal is dominant due to the large number of glances.

Observational learning would be almost impossible without gaze following. In a interesting series of experiments, Mineka et al (1984) tried to determine whether fear of snakes in rhesus macaques originated through observational or social learning. Young rhesus monkeys became fearful of snakes (this is not an innate behaviour, as it is not present in laboratory reared monkeys), when they observed their wild-reared parents showing fear responses to real, toy and model snakes. For the infant monkeys to become fearful of the snakes by observational learning, they may well have used the principles of social attention; X is producing a fearful response, and X's attention is directed to the object on the ground, therefore, they must be fearful of the object on the ground. Observational learning would seem to use, not only social attention, but also so-called *joint attention* between the individual X following the direction of conspecific Y's attention onto object Z. During observational learning or conditioning, the observer (X) determines where the observed (Y) is looking, and what Y is looking at, to be able to learn something about that object.

Laboratory studies of gaze following and joint attention *per se* are limited to a small number of species. The ability to gaze follow has been demonstrated most successfully in human infants. The age at which an infant first follows another's gaze is controversial, ranging from 6 to 18 months of age (Butterworth and Cochran 1980, Butterworth and Jarrett 1991, Corkum and Moore 1994, Scaife and Bruner 1975). These age differences may be due to differences in methods (variation in angle of gaze, the use of an experimenter versus the infant's mother) or in the definitions. Before 12 months old, human infants follow their mother's gaze but do not direct their attention to the object of her attention. At around 12 months old, infants begin to follow the gaze of their

mother towards particular objects in their visual field, and at around 18 months old they can direct their attention to objects outside of their field of view (e.g. behind them, Butterworth 1991).

The clearest evidence for the ability to follow gaze in non-human primates comes from experimental work on the great apes, in particular studies with chimpanzees. Povinelli and Eddy (1994, 1996a, b, 1997) have concluded that chimpanzees can follow a human experimenter's gaze. Povinelli and Eddy trained chimpanzee subjects to enter an experimental room, and respond to an experimenter by placing a hand in front of the experimenter for a food reward (which signified the end of a trial). Once trained to do this, the human experimenters performed prepared attention sequences for the subjects. The three conditions were 1) eyes and head, where the experimenter shifted his head and eye gaze to behind and to the left or right of the subject. The second condition was similar to the first, but the experimenter only shifted the direction of his/her eyes. The final condition was no change in attention. These three conditions were randomly assigned to test sessions. In the eyes and head condition, 50% of the trials (10 trials in each of 8 test sessions), elicited a gaze-following response from the subjects to the correct side, and in the eyes only condition, 30% of the trials elicited a gaze-following response to the correct side. Povinelli and Eddy interpreted this as shared or joint attention on the part of the chimpanzee subjects.

In a further series of experiments, Povinelli and Eddy (1996b) obstructed the subjects' line of sight with an opaque shield. The experimenters used head and eyes to look at an object out of sight of the subjects (on the same side as the experimenters behind the shield). Subjects could follow the experimenter's line of sight to the unseen object (i.e. the subjects would look at the point on the opaque barrier where the experimenter's line of sight hit the barrier). This ability may be important when trying to extrapolate information from other's attention, when the focus of attention is out of sight.

The presence of gaze following in chimpanzees and absence in Old and New World monkeys has been replicated by other investigators. Itakura (1996) recently studied eleven species of prosimians, monkeys and apes in their ability to follow a human

experimenter's gaze (eyes, head and pointing in a corresponding direction). Only the orangutan and chimpanzee subjects made greater than 70% correct responses, with the orangutan making 100% correct responses. This may be attributed to enculturation of the orangutan as suggested by Carpenter et al (1995) for chimpanzees. The non-ape subjects (brown lemur, black lemur, squirrel monkey, brown capuchin, white-face capuchin, stump-tailed macaque, rhesus macaque, pig-tailed macaque, tonkean macaque) did not respond above chance level.

A number of primate species have been shown experimentally to follow other cues to another's attention such as pointed fingers. These results are interesting because in the wild no non-human primates use or follow pointing cues. Blasche and Ettlinger (1987) trained rhesus monkeys to point at one of two boxes (one of the boxes was baited by an experimenter out of sight of the subjects). Next, an experimenter baited one of the boxes in the presence of the monkey subject. The monkey gained the food reward if it pointed to the baited box. Finally, the subject had to perform a role-reversal where the experimenter pointed at one of the boxes and the subject had to choose the correct box to gain the reward (see also Anderson et al 1995, 1996). The monkeys learnt to point to the box chosen by the experimenter after an average of 428 trials and learnt to choose the box indicated by an experimenter by 100 trials. It is unlikely that the subjects were pointing at the boxes, but were reaching towards them using the whole hand, as they never extended the index finger (as deemed a crucial component of pointing by Povinelli and Davis 1994). Hess, Novak and Povinelli (1993) reported a 16 year old hand-reared rhesus monkey who spontaneously pointed at objects and events. Again, it is unclear whether the monkey pointed at object using the index finger of her hand, rather than just the whole hand (using the whole hand suggests reaching for objects, not directing other's attention towards objects).

Orangutans (Call and Tomasello 1994b) and chimpanzees (Leavens et al 1996) have also been shown to follow pointing (either an extended index finger or a chin raise and glance), used to direct attention to objects. Call and Tomasello (1994b) found that one captive and one enculturated orangutan would spontaneously point to a baited box containing food. An experimenter baited the box in the presence of the subject and then

left the room. A second experimenter entered and waited for a response from the subject. The experimenter was naive as to the location of the food. The experimenter required that the subject pointed to a tool, which the experimenter would give to the subject to reach the baited box. The tool (a rake) had previously been used by the subjects to retrieve food (Call and Tomasello 1994a). The enculturated orangutan pointed to the tool, then to the baited container (above chance). The captive orangutan did not point to the tool, only to the baited box. A second captive orangutan, was tested and performed by directing the experimenter's attention to the tool and the box. The subjects were then tested for their levels of comprehension. An experimenter entered the room and baited one of three containers, pointed at baited container and then left. A second, naive experimenter entered the room and waited for the subject to point to the baited container. Again, the enculturated orangutan pointed to the baited container (on 33/63 trials). The captive subject did not perform above chance.

Leavens et al (1996) tested the responses of a captive chimpanzee who would vocalise, point with the index finger and alternate gaze between food and an experimenter, when the chimpanzee's food was dropped. Leavens et al found that the subject pointed 175 times (out of 18 hours observation) when the experimenter was present. During 76% of instances the subject also used gaze alternation. The subject also tended to point to non-food objects with the whole hand, but to food objects with the index finger. This subject was not language trained, enculturated or trained to point.

Anderson, Sallaberry, & Barbier (1995) investigated three capuchin monkeys (*Cebus apella*) for monkey's use of human attention cues in the laboratory. This paradigm was replicated with three rhesus macaques by Anderson, Montant, & Schmitt (1996). Both studies used a forced choice paradigm in which the monkey was allowed to choose one of two wells. A human experimenter would stand between and behind two covered food wells and demonstrate attention to the baited food well using different cues; "pointing only", "gaze only" (which included both head and eye cues), and "gaze and pointing" (combining both these cues). None of the macaque or capuchin subjects could be trained to use the "gaze only" cues to guide choice of food well. Two subjects of each species could be trained to use either "pointing only" or "gaze and pointing". It is

likely that the success with the "gaze and pointing" situation can be attributed to cues arising from pointing rather than the monitoring of gaze direction cues. Pettigrew, Forsyth and Perrett (1993, unpublished studies) using a similar protocol, obtained equivalent results. Despite extensive training (>100 trials) they found 4 out of 6 rhesus monkeys failed to learn the rule that the head and gaze direction of a human experimenter predicted the location of food reward.

In a gaze paradigm similar to that of Anderson et al (1995, 1996), Itakura and Tanaka (1997) found that chimpanzees, an enculturated orangutan and human infants (3-4 years old) could all use gaze (head and eyes) cues (near and close to the baited food wells), pointing and glancing (eyes only directed towards the food wells) to chose the well baited with food. The responses of all subjects appeared to be spontaneous, not requiring learning. Povinelli et al (1997) have also tested chimpanzees with a paradigm similar to that used by Anderson et al (1995, 1996). They found that the chimpanzee subjects could not determine which well was baited with food when using the experimenter's eyes only as a cue. When the experimenter's head and eyes were directed towards the baited well or slightly above the well, the subjects responded well above chance. The subjects could also follow active gaze (head and eyes, not eyes only), i.e. attention initially directed to between the two wells then shifting gaze to the baited well. The negative glancing (eyes only) result reported by Povinelli et al (1997) could have differed from the positive glancing result in the Itakura and Tanaka (1997) study due to the age, experimental experience and enculturation of the different sets of subjects.

Recently, Itakura and Anderson (1996) reported success training one juvenile capuchin monkey to use the experimenter's head direction to choose between two presented objects. In general, however, it seems that macaque and capuchin monkeys do not readily utilise attention cues from human demonstrators.

9.1.5 Aims of study

The study presented in this chapter attempts to resolve the differences between the physiological evidence of macaque brain mechanisms processing gaze cues (see

Chapters II and VII) and the lack of behavioural demonstration of gaze following in captive macaques. An experimental paradigm was constructed which would not require extensive training and which would specifically record the responses of monkey subjects viewing another individual's gaze behaviour. This paradigm used conspecific stimulus monkeys to provide attention direction cues and measured the spontaneous eye movements of test subjects, rather than requiring the subjects to provide an action for a reward (as neurons in the STS also respond to differences in species' faces, see Chapter VIII).

9.2 Methods

9.2.1 Subjects

The subjects were two male rhesus macaques, Steve, aged 4 years, and Terry, aged 3 years, who were also subjects in ongoing neurophysiological studies that required stable eye movement recording (see Perrett et al. 1985b for details of neurophysiological procedures). The subjects had previously been shown videofilm of conspecific monkeys and other animals. They had also been exposed to slides and videodisk images of humans, monkeys and other animals. The subjects were born and reared in a social colony of rhesus monkeys. During the period of the experiment, the subjects were housed individually but remained in auditory and visual contact with the other monkeys. The subjects were familiarised with the test room and a primate chair with head restraint. During testing fruit juice was available *ad libitum*. All experiments were performed under a UK Home Office Project and Personal License and all experiments were regulated by the University of St Andrews Animal Code of Practice.

9.2.2 Test stimuli

Test stimuli were created by videotaping (Panasonic SVHS video camera) a stimulus monkey sitting at a square window (width 26.5 cm) with the area surrounding the window blacked out. The stimulus monkey was filmed maintaining attention in one

direction (either down left [DL], down right [DR], up left [UL] or up right [UR]). The stimulus monkey was attracted to look intently in one direction by presenting interesting stimuli at the desired locations. A JVC colour monitor was set up on a stand in one of the four desired attention locations (DL/DR/UL/UR). From the stimulus monkey's perspective the left and right positions of the monitor were separated by 120 degrees. Various images were presented over the monitor, played on an Akai Video Cassette Recorder (VCR), including videotaped images of various animals in a zoo, cartoons and pictures of monkeys. Particular hand-puppets, face masks and toys were also presented from behind an occluder to achieve the same purpose. These methods were sufficient to allow video recording of 20 segments of film (5 each of DL, DR, UL and UR), which would be converted to test trials. These segments were edited using a Panasonic SVHS VCR (NV-FS200B) and a Panasonic VHS video mixer (WJAVE7) to blank off the area on either side of the window, leaving only the centrally positioned stimulus monkey visible.

Two objects were added to each trial segment. The objects were identical mirror images of each other and were recorded onto videotape at the same time and at opposite lateral corners of the screen. This was achieved using a Fairlight CVI (computer-video effects machine). One object was filmed using a Panasonic SVHS video camera (F10CCD) at either the bottom left or top left of the screen, and mirrored about the centre of the screen (Fairlight CVI). This provided the illusion that two identical objects were entering the screen at the same time and at the same mirrored spatial location, for example, one object enters bottom left, while the other enters bottom right. A different object was used for each trial. The objects were all novel to the subject, all approximately the same size and made small movements up and down.

The specific object or position that the stimulus monkey was attending to is referred to as the target object or attended target position (T), and the object at the opposite position as the distracter object or non-attended distracter position (D). The contents of the central window are referred to as stimulus monkey, and everywhere else on the screen is referred to as elsewhere (E). An idealised example of a frame from the test tape is presented in Figure 9.2. The projected distance between target and distracter

Figure 9.2. Spatial representation of test stimuli. The stimulus monkey is positioned relatively central attending down left to the target object and away from an identical distracter object (condition 1, Monkey and Objects time period). During testing, the subject's eye movements and a frame/time code are mixed onto a copy of this test-tape (not shown). For test stimuli eyes, head and body of the stimulus monkey had the same direction of orientation.

on the actual test tape was 40 degrees (physical distance 150 cm) and the physical distance between the stimulus monkey's head and the target was on average 90 cm (minimum 80 cm, maximum 100 cm). During some trials the stimulus monkey's head moved towards and away from the target. Measurement showed that on average across trials the stimulus monkey's head was marginally closer to the distracter than to the target. In all trials the orientation of the stimulus monkey's gaze was identical to the orientation of the head.

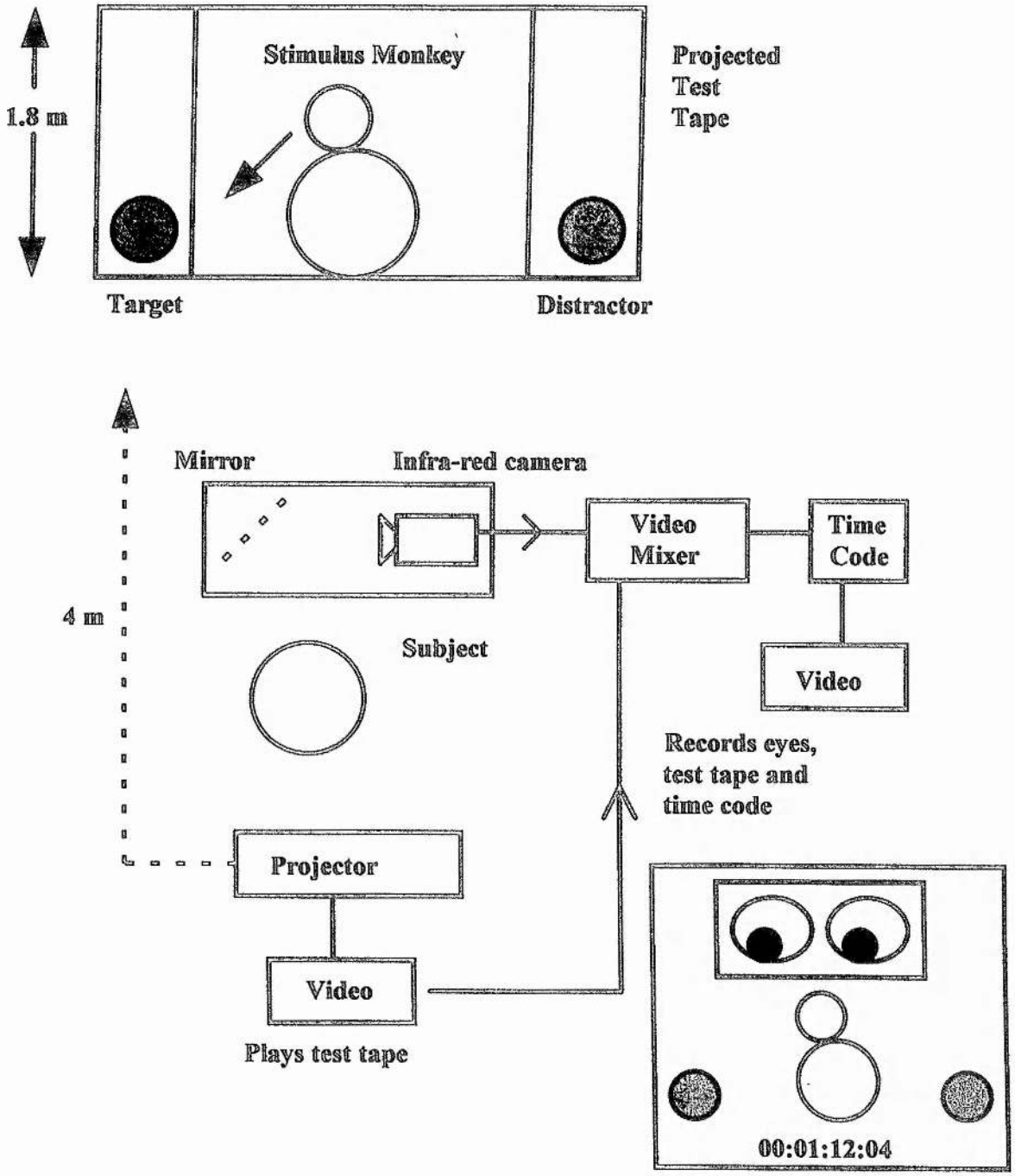
Two final test tapes were prepared. Condition 1 included 20 trials with target and distracters down left and down right. Condition 2 included 20 trials with target and distracters up left and up right. The left/right position of the target and distracter were randomised across trials.

9.2.3 Experimental Procedure

The subject was seated 4 m from the projector screen, at the same height as the projected stimulus monkey. An infra-red camera and a half-silvered mirror were attached to the front of the primate chair. This arrangement allowed the subject's eye movements to be videotaped while viewing test stimuli through the mirror (see Figure 9.3). A VITC time-code generator and frame counter (Horita VG50) allowed the addition of a time and frame code to the bottom of the eye movement recording tape. The video stimuli were projected in a darkened room to avoid any visual distraction for the subject. The test tape was presented on a VCR (Panasonic NV-FS200B), with an output to a Sony colour video projector (VPH-1041 QM). The output from the eye movement camera was video-mixed (Panasonic VHS video mixer, WJAVE7) onto a copy of the test stimuli tape with the frame code, and recorded onto VHS tape on a VCR (Panasonic NV-FS200B).

Three time periods were present during each trial. A 1.0 second tone preceded the beginning of the trial where the stimulus monkey appears (Monkey Only). After 2-3 seconds, the objects appear (Monkey and Objects). The stimulus monkey and objects remained on screen for 7-9 seconds, after which the stimulus monkey disappeared off screen. The objects remained on screen for a further 2-3 seconds (Objects Only). There

Figure 9.3. Recording and stimulus presentation set-up. The test video was presented on a large white screen 4 meters from the subject. The subject's eye movements were recorded by an infra-red camera positioned in front of the subject. The eye movements were then mixed onto a copy of the test tape for off-line analysis. A frame/time code is also added to this copy of the test tape.



was an inter-trial period of 5-6 seconds before the next tone and trial. Trials varied in duration, due to changes in the length of time which the stimulus monkey's attention was captured in the test direction during the original filming of the test tapes.

9.2.4 Scoring gaze direction

For each trial, the frame counts (1 frame = 40 ms) of the critical events (trial begins, targets appear, stimulus monkey disappears and trial ends) and stimulus monkey's orientation were recorded onto score sheets by one observer by projecting the test video with the stimulus monkey, objects and eye movements present.

Analysis of the location of inspections was performed by two observers 'blind' to the orientation of the stimulus monkey. This analysis was achieved by blanking off the region of the test tape containing the stimulus monkey with the video mixer. The resulting image contained the subject's eyes and the objects when they appeared. Analysis was performed on the test video (minus the central region) projected onto the screen so that the distance between the eyes in the projected image of the subject's face was 18 cm (i.e. 32 cm between pupils).

Attribution judgements were made by blind scorers for each of the subject's inspections. A fixation was defined as the subject's eyes remaining static for at least 2-3 frames duration (80-120 ms). Multiple successive fixations on different regions of the same object without intervening fixations of other objects and/or positions were scored as a single inspection. During a saccade the subject was scored as not looking at anything. Inspections were attributed to one of four areas: 1) left target, 2) right target, 3) centre (stimulus monkey) and 4) elsewhere. The position of each inspection and its frame count were recorded for analysis.

An off-line analysis, which combined blind scoring of inspections (by one rater) and records of stimulus monkey orientation, reclassified the 4 inspection positions to inspection of target, distracter, stimulus monkey and elsewhere. Inter-observer reliability was calculated for a sample of 20 trials by correlating the number of inspections attributed to different positions per trial by two blind scorers analysing videos

independently. The independent blind scoring correlated highly for the different positions; stimulus monkey, Pearson's r^2 (19) = 0.59, $p < 0.01$; target, r^2 (19) = 0.69, $p < 0.01$ and distracter, r^2(19) = 0.76, $p < 0.01$.

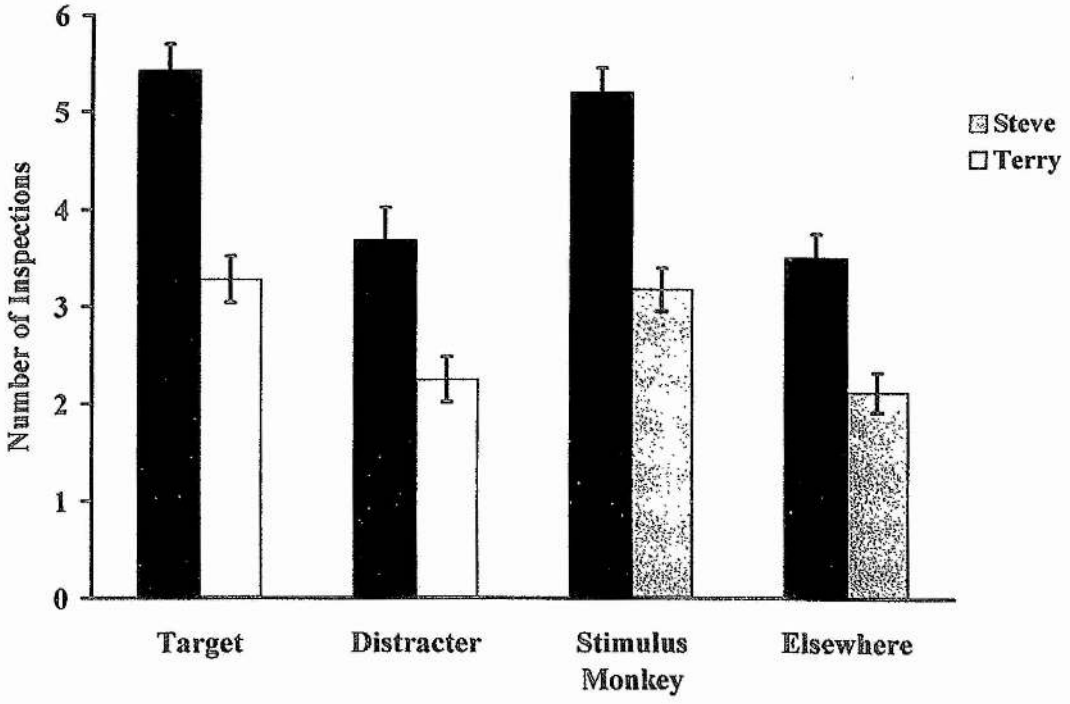
9.2.5 Data analysis

From the score sheets, the mean number of inspections made of each of the four positions were calculated for each trial. The duration of each inspection was also calculated from the frame count. The number of inspections and duration per inspection were compared for the whole trial using a three-way Analysis of Variance (ANOVA) where the factors were subject (Steve, Terry), condition (Down/Up) and position (T, D, M, E), and Newman-Keuls (NK) *post-hoc* tests were used to determine specific significant differences. The number of inspections at each position (T, D, M and E) was also measured for each individual time period. For each time period, the proportion (%) of inspections of the target plus distracter positions were compared using a Binomial test, combining data for each subject.

9.3 Results

Both subjects' (S, T) eye movements were recorded for condition 1 (down) and condition 2 (up) for 20 trials each. The results were analysed for the whole trial using a three-way ANOVA (subjects, condition (down/up) and inspection position as main factors). There was a significant main effect of position on the number of inspections made ($F(3,3) = 16.05$, $p < 0.05$). Of greatest importance, the number of inspections on the target position was significantly greater than the number of inspections on the distracter position (NK, $p < 0.05$). Figure 9.4 illustrates that although Steve made more inspections than Terry (main effect of subjects $F(1,76) = 81.46$, $p < 0.001$), the pattern of inspection across different positions was constant across the 2 subjects (no interaction between subjects and position ($F(3,228) = 1.32$, $p = 0.27$).

Figure 9.4. Pattern of inspections within test stimuli. Mean number of inspections (+/- SEM) made to each position (target, distracter, stimulus monkey and elsewhere) for the Whole trial. Data is averaged for the 40 trials (in conditions 1 and 2) separately for each of the two subjects. Note the pattern of inspections across positions is the same for both subjects even though Steve makes more inspections overall compared to Terry.



Of less importance, there was no significant main effect of condition ($F(1,1) = 33.28, p = 0.11$), as the number of inspections was not different between the up and down conditions. Other interactions between the main factors were all non-significant (subjects and condition ($F(1,76) = 0.18, p = 0.68$), condition and position ($F(3,3) = 1.55, p = 0.36$), subjects, condition and position ($F(3,228) = 1.0\ p = 0.39$).

Behaviour during the individual time periods was analysed using a Binomial test. The number of inspections made by each subject of the target position (T) or the distracter position (D), for each time period for the total 40 trials, was calculated as a percentage of the total number of inspections of the target position plus the distracter position (T+D). For the Monkey Only time period, the proportion of inspections of the target position was significantly greater than that for the distracter position (Binomial test, $Z = 4.7$, $p<0.01$). During the Monkey and Objects time period, the number of inspections of the target was also significantly greater than that for the distracter (Binomial test, $Z = 2.6, p < 0.05$). There was no significant difference between the proportion of inspections of the target and distracter for the final Objects Only time period (Binomial test, $Z = 0.9, p = 0.18$). See Figure 9.5 for these results.

The number of frames at each of the four positions, for the two subjects and conditions were analysed using a three-way ANOVA. There was no significant main effect of position ($F(3, 3) = 3.6, p = 0.16$) and therefore no difference between the number of frames spent looking at the target and the distracter (see Figure 9.6). There was no significant main effect of subjects ($F(1, 76) = 1.52, p = 0.22$) or condition ($F(1, 1) = 2.41, p = 0.36$) and no interaction between subjects and condition ($F(1, 76) = 0.51, p = 0.48$), or between condition and position ($F(3, 3) = 0.94, p = 0.52$). There was a significant interaction between the subjects and position ($F(3, 3) = 5.5, p < 0.001$). Steve spent significantly more time looking at the target than the distracter (NK, $p < 0.05$), whereas the difference for Terry was non-significant.

The duration of inspections over the whole trial was further analysed using comparable methods to those above, with time spent inspecting the target and distracter expressed as a proportion of total time spent inspecting both the target and distracter for each of 40 trials. The average of both subjects indicated that subjects spent a greater

Figure 9.5. Proportion of target and distracter inspections across different trial periods. **Upper:** stimuli during the successive periods of the trial (Monkey Only, Monkey + Objects, Objects Only). **Lower:** mean proportion of inspections made to the target (T) and distracter (D) positions (expressed as a percentage of T+D) for each trial period.

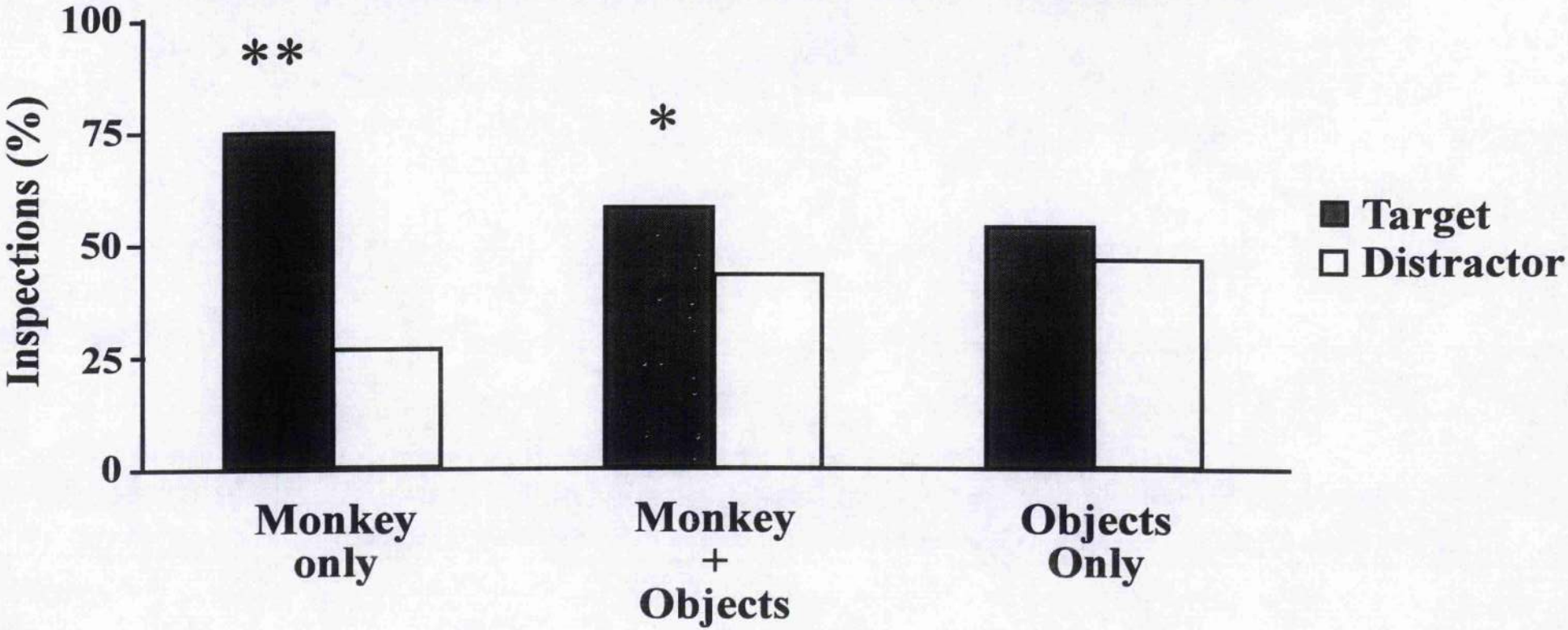
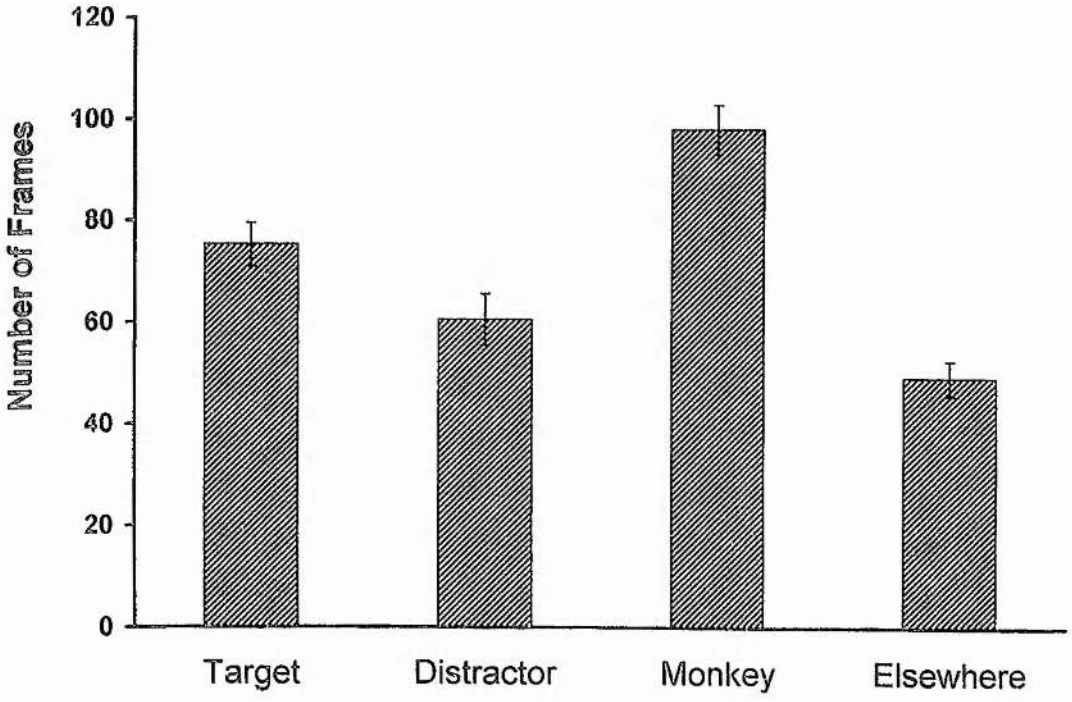

100
75
50
25
0
Inspections (%)
**
*
Target
Distractor
Monkey only
Monkey + Objects
Objects Only

Figure 9.6. Duration of inspections. The average number of frames, +/- SEM spent inspecting the different stimulus positions for the Whole trial. Data for the 40 trials for each of the two subjects in conditions 1 and 2 has been averaged.



proportion of time inspecting the target position than the distracter position (Binomial test, $Z = 12.2$, $p < 0.01$).

9.4 Discussion

The results presented above provide the first experimental evidence that rhesus monkeys follow another monkey's gaze, and use their gaze cues to orient their own attention to a specific object. The subjects followed the stimulus monkey's line of sight before any objects were presented, and inspected the attended target object more than the identical non-distracter object when the objects appeared. These results contrast with a recent study of non-human primate gaze following by Itakura (1996), as they provide evidence that monkeys, like great apes (Povinelli and Eddy 1994, 1996a, b), can follow gaze cues onto specific objects.

In the first part of the trial (Monkey Only), the stimulus monkey exhibited intense interest to a particular point in space and the subjects appear to have followed the stimulus monkey's direction of attention to this position. In terms of the definition stated in the introduction, the subjects have followed the stimulus monkey's gaze, but are not joined in attention with the stimulus monkey. In the second time period (Monkey and Objects), a specific object appeared as a focus of the stimulus monkey's attention. The subjects looked significantly more at this target object than at the alternative distracter object. During this section of the trial, the subjects and the stimulus monkey had joint attention, as they both attended the same object (Perrett and Emery 1994).

One might have expected that any salience that the target object gained from 10 seconds attention of the stimulus monkey would persist into the final part of the trial (Objects Only), when the stimulus monkey disappeared and only the objects remained. This was not the case. The trend for the target object to be inspected more frequently that the distracter in the final period of the trials did not reach significance. Rhesus monkeys follow conspecifics' gaze to objects but may not understand the mental significance of another's attention (i.e. that the other individual is interested in the object).

This would be compatible with a *primitive orienting reflex* (Povinelli and Eddy 1996a) where monkeys follow other's gaze cues automatically.

Methodological differences may explain the discrepancies in results between this and the Itakura (1996) study. Itakura attempted to determine whether prosimians, monkeys and apes were able to follow the gaze, head and pointing cues of a human experimenter. Itakura required a large angle of gaze change (90 degrees) before scoring the subject's gaze following positively. This angular change is larger than that required of the subjects in the present study. Furthermore, before providing the attention cues, the experimenter attempted to gain eye contact with each subject. Monkeys do not readily look into the eyes of humans or conspecifics (especially a more dominant individual) but apes do (Redican 1975). Apes are therefore more likely to look into the eyes of humans and therefore are more likely to use gaze cues. Indeed, apes may learn to utilise human gaze cues through socialisation or enculturation, during extensive interaction with human experimenters and caregivers (Carpenter, Tomasello and Savage-Rumbaugh 1995). In contrast to apes, macaque monkeys may be less willing to use the gaze of human experimenters in operant tasks because humans are perceived as more threatening. Any reluctance of macaques in this respect was circumvented in the present study by using videofilm of conspecifics as stimuli.

The eye region is particularly salient in primate species (Argyle and Cook 1976, Keating and Keating 1982, Perrett and Mistlin 1990, Chapter VII). Baron-Cohen (1994) has proposed a cognitive (and neural) module, the Eye Direction Detector (EDD) which codes attention direction from eye gaze alone. Perrett and Emery (1994) note that the brain mechanisms for detecting attention direction (DAD) use multiple visual cues including eye gaze, head direction and body posture. In this study several cues to attention were oriented in the same directions. The subjects in the present study may have used eye gaze, head orientation and posture, or body posture to follow the stimulus monkey's direction of attention. The behavioural ability of monkeys to follow attention demonstrated here is consistent with the neurophysiological finding described in the introduction. Cell populations have been found which respond to direction of eyes, head and body (Brothers and Ring 1993, Leonard et al. 1985, Perrett et al. 1985, 1992, Perrett

& Mistlin 1990, Wachsmuth et al. 1994). Such cells may contribute the appropriate *neural machinery* required to process the direction of another's attention from a variety of visual cues.

An unpublished study by Tomasello, Call and Hare (1997) has confirmed the results of this study using semi-free ranging primates in a large enclosure. Tomasello et al found that five species of non-human primate; rhesus, stumptailed and pigtailed macaques, sooty mangabeys and chimpanzees; could follow the gaze cues of conspecifics. The experimenter waited for two conspecifics to be proximal to one another, then the experimenters would attempt to gain the first conspecific's attention by holding up some food. The experimenter would then record the second conspecific's (named the subject) behaviour. The experimental trials were spilt into two sections; questionable and valid. The questionable trials were designated as trials where the conspecific looked at the food, but the subject did not notice the conspecific's attention cue, but did look at the food. The valid trials were designated as trials where the subject looked at the conspecific (and hence gaze cues) and then looked at the food. In the control trials, the food was presented when only the conspecific was present. Tomasello et al found that in all species tested, the subjects looked at the food on a highly significant number of valid trials (79-100%). Interestingly, the stumptailed macaque subjects responded 100% correctly (significantly better than chimpanzees). Stumptails may use gaze cues more often in affiliative gestures than other species. This may be due to the gentle, relaxed manner with which stumptailed macaques interact with conspecifics (such as alerting others to danger; de Waal 1989).

Primatologists have begun to test non-human primates' knowledge of the mental significance of attention (Gomez 1991, 1996, Anderson et al. 1995, 1996, Povinelli 1996, Whiten 1997a, b). Even though monkeys can spontaneously follow the gaze cues of other monkeys, monkeys' abilities to utilise gaze cues in experimental tasks appears more limited than ethological observations might suggest. Povinelli and Eddy (1996b) suggested that the ability to understand the mental significance of another's gaze is a dissociable ability from simple gaze following, although one may be a precursor to the other (Baron-Cohen 1994, Perrett and Emery 1994). Whiten (1996a) has speculated that

behaviour-reading, or inferring goal-directed behaviour, emotion and intention from external perceptual signals and a representation of an individual's behavioural patterns, may have developed through evolution into a 'mind-reading' ability or a 'theory of mind mechanism' (Premack and Woodruff 1978).

Neurons in the STS and basolateral (BL) complex of the amygdala are selective to the sight of a second individual's eyes, heads and bodies horizontally oriented to one specific view (see Chapters II and VII) The amygdala (and probably STS) appear to have evolved throughout the evolution of the primates to process highly processed visual social signals. This assumption would appear to be suggestive as results of the comparative analysis (Chapter V) show strong relationships between social groups size and the volume of the BL complex of the amygdala). Cues of another's attention may be used to process another's intentions within a purposive behavioural framework, rather than a mentalistic framework. Such a high level method of analysing another's behavioural patterns may be a precursor to the analysis of another's mental state (as suggested by Whiten 1996a).

Chapter X

General Discussion

The results described within this thesis suggest a role for the cortex of the superior temporal sulcus (STS) and the lateral basal nucleus (LB) of the amygdala in coding for aspects of macaques' social behaviour. In particular, these structures are involved in the perception of visual social signals, that may aid an individual in understanding another individual's purposive behaviour.

The main results of this thesis were as follows:

(1) Lesions of the amygdala, anterior temporal cortex and orbitofrontal cortex in monkeys cause various deficits in processing information about other individuals. Perceiving others' appearance, actions, purposive behaviour and emotions (social perception) appears to be compromised by lesions of the anterior temporal cortex and amygdala, and using social information in complex situations (social cognition) appears to be affected by lesions of the orbitofrontal cortex. Unfortunately, the specific control of social perception and social cognition by these three regions is not known from lesion studies, as the lesions were unspecific to individual amygdala nuclei or cortical region.

(2) The anatomy of the individual amygdala nuclei suggests differences in function between the different nuclei. This was tested using a novel method of analysing the inter-relationships between anatomical areas. Non-metric multidimensional scaling (NMDS) was used to analyse the similarities between different brain areas' connectional architecture. Statistical analysis (e.g. NMDS) of the similarities in connectivity between amygdala nuclei or cortical regions (an objective measure) enabled a subjective measure of the relatedness between areas to be proposed. NMDS (and cluster analysis) found that the individual nuclei of the amygdala differed in their connectivity with other brain areas

and that the amygdala split into three groups; the basolateral complex (BL), the centromedial complex (CM) and the peripheral nuclei. The BL was positioned close to areas of the sensory cortex involved in complex levels of sensory processing, such as the STS which processes features such as faces. This suggests that highly processed sensory (social) information enters the BL complex. The CM complex was positioned close to the prefrontal cortex which suggests that neurons of the nuclei of the CM complex project out of the amygdala, passing on highly processed social information to the prefrontal cortex. The LB nucleus is separated from the rest of the BL complex (placed next to areas within both processing streams of the cortical visual system). This suggests that the LB nucleus may be the most important area within the amygdala which communicates with the visual system. This is also indicated by the profuse back connections from the LB nucleus to the occipital lobe (including primary visual cortex).

(3) The probable link between the LB nucleus and social behaviour was tested further across a large number of primate species (haplorhines and strepserhines) using the comparative method. The volume of the LB nucleus, the BL and CM complexes and the amygdala were correlated with measures of primate social cognition (e.g. social group size, number of females in a group, percentage time spent grooming) and also with indices of ecological processing (percentage fruit in the diet and home range size). The LB nucleus was the only structure to correlate significantly with all indices of socio-ecology. The role of the LB nucleus in behaviour may be more generalised than the rest of the nuclei of the amygdala. High correlations between the volume of the LB nucleus and social cognition and between the volume of LB nucleus and ecology suggest that this nucleus may be functioning in attributing value (reward) to
objects. For example, information concerning the basic perceptual attributes of social interaction (such as facial expressions, body movements, vocalisations, etc.) may reach the amygdala via the lateral (L) nucleus, but the function of interpreting the interaction as rewarding or aversive may be performed by the LB nucleus. Similarly, information concerning basic perceptual details about the location, smell and taste of food (fruit, leaves, nuts, meat, etc.) may be processed by the anterior temporal cortex and L nucleus.

(4) The above results would suggest that recording from single units within the LB nucleus would be futile when studying the neural mechanisms of social perception. Complex visual social information appears to reach the L nucleus from the STS, so further processing of complex features may not be required during the next step of the processing pathway in the amygdala (the LB nucleus). It is possible that the L nucleus is integrating sensory information about complex objects (their smell, appearance, taste and sound). The coding of visual information in the STS is extremely complex. Recording within this region of the awake macaque brain found neurons which were responsive to multiple features of faces (monkey, human and other species' faces), bodies and body parts; static or in motion; and interacting with other objects in the environment. These neurons may function in processing information about other individuals and their actions within the environment. Such a type of processing may enable an individual to predict anothers' behaviour in relation to the world and the viewing individual, such as in forms of social interaction. How similar levels of social information processing may be compromised in the psychopathological disorder of autism is discussed below.

(5) Some of the cells found in anterior STS were responsive to the sight of the head and/or the eyes. It is unlikely that neurons selectively responsive to one view of the head are used to code for the appearance of the head. Intermediate head views from the 4 (0^0, 90^0, 180^0 and 270^0) or 8 (0^0, 45^0, 90^0, 135^0, 180^0, 225^0, 270^0 and 315^0) canonical views, such as 22.5^0 are represented by single neurons. It would seem logical to suggest that such cells are coding for the appearance of the head directed towards one view. No cells have been reported where their response is contingent on only one direction of the eyes. This would tend to indicate that the eyes are not in themselves important indicators of attention direction in macaques. The behavioural literature also reports negative findings of eye gaze following in non-ape species. This lack of evidence may be due to the fact that the eyes have a large emotional meaning attached to them for the majority of Old and New World monkeys. Eye gaze, in the form of a direct stare is used as a threatening gesture. Monkeys may be unable to use other forms of information from the eyes, such as references to objects and locations in the environment or as a means of affiliation, as seen in the great apes and humans.

If monkeys did use information from the bodies of other individuals to learn about things in the world, it is likely that they do not use eye gaze specifically, but do use the direction of the head and/or body. This would also appear to be the case from the large number of single neurons which are selectively responsive to one view of the head. There were contradictions in the literature on the ability of monkeys to use others' gaze (eyes or head). Ethological studies suggested that monkeys do use gaze, whereas laboratory studies suggested that monkeys do not use gaze. The results of the study described in the last chapter suggest that monkeys use conspecifics' head (and possibly eyes) as indicators of their attention. This form of processing has been suggested to be a precursor step to learning about anothers' mental state (see below), but even as a precursor stage the level of information which may be transferred using this means of communication is complex.

The anterior STS may therefore function as an advanced processor of complex features, which may be utilised in social cognition. The next steps in the processing pathway in the amygdala, i.e. the BL complex (in particular the LB nucleus) are unlikely to be processing basic perceptual features of an object, as more complex attributes of biological objects appear to be processed by neurons within the STS.

These results have may important implications for the disorder of autism. Baron-Cohen (1994) stated that the ability to attribute mental states to other beings or the 'theory of mind mechanism' (ToMM) is reliant on a number of precursor modules. The first module, the 'intentionality detector' (ID) functions to interpret others' behaviour in relation to objects in the environment (i.e. actions with an end purpose; see Chapter VII). For example, perceiving a hand reaching towards an object, the viewer can predict the outcome of the action; the hand will reach the object and pick it up. This is dependent on a number of variables, such as the configuration of the fingers in the hand, the size and weight of the object, the function of the object, etc.). Neurons in anterior STS have already been described which respond to the motion of bodies and hands towards and away from objects. These neurons may form part of an ID.

The second module which would be required for ToMM to function correctly is an 'eye direction detector' (EDD). This would detect the presence of the eyes as a class of object and the direction in which the eyes are directed. Similar to the ID, some cells

within the anterior STS have been found which respond to the presence of the eyes and to different eye gaze directions. As stated earlier, no cells have been found which respond to only one eye direction (all cells respond to multiple directions, whilst are also inhibitory to one direction). Perrett and Emery (1994) therefore proposed a 'direction of attention detector' (DAD), based on the neurophysiological evidence. This module would function in similar ways to the EDD, but would enable a viewer to infer anothers' attention direction from multiple cues, such as the eyes, the head or the body. Such a system would be strictly hierarchical, where the eyes would be the best indicators of attention direction, followed by the head and then the body. In situations where two direction cues are in conflict (e.g. when the eyes are looking to the left, but the head is looking forward) the eyes would be presumed to be correct indicators to attention direction.

The final precursor to ToMM would be the 'shared attention mechanism' (SAM). This module enables the analysis of triadic relationships between a viewer (X), an observed individual (Y) and an object or location (Z). For attention to be shared, X and Y must both be directing their attention to object Z and must have knowledge that the other is aware of their attention and vice versa. A more basic form of this level of processing (joint attention) was discussed in chapter IX, where both X and Y's attention was directed onto the same object. No neural correlates have been found for either shared or joint attention, i.e. no cells were found to be significantly different in their response between perceiving a head directed to one view and the same head view with attention towards (or away) from an object. Such cells may not exist in the rhesus monkey brain and this may go some way to explaining why there is no positive evidence which suggests that macaques can attribute mental states to others. It appears that they do not have the neural architecture required for such feats of social information processing.

Individuals with autism seem to be deficient in processing shared attention. It can reasonably be predicted that the brains of normal functioning human adults and children have neurons which correspond to those found in rhesus macaques and which correspond to the three modules described above (also including neurons which function in the

ToMM). It is, however, more difficult to say anything about the brains of autistic individuals, when there is no convincing evidence which suggests that these individuals are affected at gross neural levels (i.e. which can be detected on positron emission tomography; PET or magnetic resonance imaging; MRI scans). Three possibilities arise from a neurological explanation of functional deficits in autistic individuals. First, the brain systems which code for shared attention (amongst many other social and non-social deficits) fail to develop properly or at all. Second, damage may occur to precise systems of neurons at the microscopic level. Finally, there may be a disruption of the individual firing patterns of neuronal circuits. All three possible explanations unfortunately are difficult (if not impossible) to investigate under present situations, so continued work using non-human primates is essential to further investigate the subtleties of the neural coding of social perception and cognition.

There is a problem with extrapolating results of studies from non-human primates to humans. The effects of lesions in monkeys appear to cause different effects from lesions to the same brain area in humans. Amygdala damage in humans after neurosurgery or disease, causes very specific, but minor deficits in socio-emotional behaviour, whereas in monkeys, the deficits are more generalised and substantial. For example, the processing of others' expressions of fear (visual and auditory) is pronounced in human patients with extensive amygdala damage, but other socio-emotional behaviours are relatively unaffected (Young et al 1995, Scott et al 1997). However, many behaviours have not been tested. Processing others' gaze, however, appears to be compromised equally in rhesus monkeys and humans (Young et al 1995, Campbell et al 1990, Heywood and Cowey 1992). Similar sized lesions in Old World monkeys affect many other forms of socio-emotional behaviour. This may be due in part to differences between monkey and human social behaviour or to a shift of social function from the amygdala (and other parts of the 'limbic system') to the cortex (in particular, the prefrontal cortex). Monkey social behaviour is complex (see Chapter II), but may be said to be less subtle than human social behaviour. This would make behavioural comparisons between monkeys and humans extremely difficult, as a large number of the subtle social behaviours usually available to normal functioning humans

would not be present in the behavioural repertoire of most monkeys and apes. This may explain the differences in social behaviour deficits after amygdala damage in monkeys and humans.

Future research into the neural basis of social behaviour in human and non-human primates could target a number of areas. A close examination of human social behaviour, such as from studying the human social perception and social cognition literature, may reveal a number of subtle differences between monkeys and humans, which may be utilised in studies of brain damaged human patients (see, for example, papers by the Damasio group).

When studying the effects of brain lesions on monkey social behaviour, the question of damage to adjacent brain areas or to fibres of passage must be addressed. Recently, David Amaral's group at the University of California, Davis have been attempting to lesion the rhesus monkey amygdala (and L nucleus) with an axon-sparing excitotoxin; ibotenic acid. Preliminary results (Amaral, personal communication) suggest that a large number of the deficits in social behaviour (especially affiliative behaviours) are seen after ibotenic acid lesions of the whole amygdala. Amaral's group are also using sophisticated measurements of the monkeys' behaviour to help resolve previous discrepancies between amygdala lesion effects.

Specific questions need to be raised about the precise anatomical location of the areas coding individual social behaviours. Complex levels of processing social information can be located to single neurons in the STS and amygdala. Area X may contain 15 regions, where each region may function in one behaviour. Lesioning area X will disrupt all 15 functions. It is therefore important to attempt to localise lesions to single structures. This is extremely difficult at present, especially in very small brain structures. It may be attempted by use of better lesion localisation methods, such as MRI.

References

Adolphs, R., Damasio, H., Tranel, D., & Damasio, A.R. (1996). Cortical systems for the recognition of emotion in facial expressions. *Journal of Neuroscience, 16,* 7678-7687.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A.R. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature, 372,* 669-672.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A.R. (1995). Fear and the human amygdala. *Journal of Neuroscience, 15,* 5879-5891.

Aggleton, J.P. (1985). A description of intra-amygdaloid connections in Old World monkeys. *Experimental Brain Research, 57,* 390-399.

Aggleton, J.P. (1986). A description of the amygdalo-hippocampal interconnections in the macaque monkey. *Experimental Brain Research, 64,* 515-526.

Aggleton, J.P., Burton, M.J., & Passingham, R.E. (1980). Cortical and subcortical afferents to the amygdala of the rhesus monkey (*Macaca mulatta*). *Brain Research, 190,* 347-368.

Aggleton, J.P., Friedman, D.P., & Mishkin, M. (1987). A comparison between the connections of the amygdala and hippocampus with the basal forebrain in the macaque. *Experimental Brain Research, 67,* 556-568.

Aggleton, J.P., & Mishkin, M. (1984). Projections of the amygdala to the thalamus in the Cynomolgus monkey. *Journal of Comparative Neurology, 222,* 56-68.

Aggleton, J.P., & Passingham, R.E. (1981). Syndrome produced by lesions of the amygdala in monkeys (*Macaca mulatta*). *Journal of Comparative and Physiological Psychology, 95,* 961-977.

Aiello, L.C., & Dunbar, R.I.M. (1993). Neocortex size, group size, and the evolution of language. *Current Anthropology, 34,* 184-193.

Aiello, L.C., & Wheeler, P. (1995). The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology, 36,* 199-221.

Akert, K., Gruesen, R.A., Woolsey, C.N., & Meyer, D.R. (1961). Kluver-Bucy syndrome in monkeys with neocortical ablations of the temporal lobe. *Brain, 84,* 480-497.

Allison, T., Ginter, H., McCarthy, G., Nobre, A.C., Puce, A., Luby, M., & Spencer, D.D. (1994). Face recognition in human extrastriate cortex. *Journal of Neurophysiology, 71,* 821-825.

Amaral, D.G. (1987). Memory:anatomical organization of candidate brain regions. In V.B. Mountcastle, F. Plum, & S.R. Geiger (Eds.), *Handbook of Physiology Section 1:The Nervous System Volume V:Higher Functions of the Brain Part 1.* (pp. 211-294). Bethesda,Maryland,USA: American Physiological Society.

Amaral, D.G., & Cowan, W.M. (1980). Subcortical afferents to the hippocampal formation in the monkey. *Journal of Comparative Neurology, 189,* 573-591.

Amaral, D.G., & Price, J.L. (1984). Amygdalo-cortical projections in the monkey (*Macaca fasicularis*). *Journal of Comparative Neurology, 230,* 465-496.

Amaral, D.G., Price, J.L., Pitkanen, A., & Carmichael, S.T. (1992). Anatomical organisation of the primate amygdaloid complex. In J.P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory and mental dysfunction.* (pp. 1-66). New York: Wiley-Liss.

Amaral, D.G., Veazey, R.B., & Cowan, W.M. (1982). Some observations on hypothalamo-amygdaloid connections in the monkey. *Brain Research, 252,* 13-27.

Andersen, R. (1978). Cognitive changes after amygdalotomy. *Neuropsychologia, 16,* 439-451.

Anderson, J.R., Montant, M., & Schmitt, D. (1996). Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behavioural Processes, 37,* 47-55.

Anderson, J.R., Sallaberry, P., & Barbier, H. (1995). Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Animal Behaviour, 49,* 201-208.

Andrew, R.J. (1963a). Evolution of facial expression. *Science, 142,* 1034-1041.

Andrew, R.J. (1963b). The origin and evolution of the calls and facial expressions of the primates. *Behaviour, 20,* 1-109.

Argyle, M., & Cook, M. (1976). *Gaze and mutual gaze.* Cambridge: Cambridge University Press.

Arikuni, T., Sako, H., & Murata, A. (1994). Ipsilateral connections of the anterior cingulate cortex with the frontal and medial temporal cortices in the macaque monkey. *Neuroscience Research, 21,* 19-39.

Armstrong, E., Clarke, M.R., & Hill, E.M. (1987). Relative size of the anterior thalamic nuclei differentiates anthropoids by social system. *Brain, Behavior and Evolution, 30,* 263-271.

Avendano, C., Price, J.L., & Amaral, D.G. (1983). Evidence for an amygdaloid projection to premotor cortex but not to motor cortex in the monkey. *Brain Research, 264,* 111-117.

Bachevalier, J. (1991). An animal model for childhood autism: memory loss and sociopathic disturbances following neonatal damage to the limbic system in monkeys. In C.A. Tamminga & S.C. Schultz (Eds.), *Advances in neuropsychiatry and psychopharmacology: volume one: Schizophrenia research.* (pp. 129-140). New york: Raven Press,Ltd.

Bachevalier, J. (1994). Medial temporal lobe structures and autism: a review of clinical and experimental findings. *Neuropsychologia, 32,* 627-648.

Baizer, J.S., Desimone, R., & Ungerleider, L.G. (1993). Comparision of subcortical connections of inferior temporal and posterior parietal cortex in monkeys. *Visual Neuroscience, 10,* 59-72.

Barbas, H. (1988). Anatomic organization of basoventral and mediodorsal visual recipient prefrontal regions in the rhesus monkey. *Journal of Comparative Neurology, 276,* 313-342.

Barbas, H. (1993). Organization of cortical afferent input to orbitofrontal areas in the rhesus monkey. *Neuroscience, 56(4),* 841-864.

Barbas, H., & De Olmos, J. (1990). Projections from the amygdala to basoventral and mediodorsal prefrontal regions in the rhesus monkey. *Journal of Comparative Neurology, 300,* 549-571.

Barbas, H., & Pandya, D.N. (1989). Architecture and intrinsic connections of the prefrontal cortex in the rhesus monkey. *Journal of Comparative Neurology, 286,* 353-375.

Barnes, C.L., & Pandya, D.N. (1992). Efferent cortical connections of multimodal cortex of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology, 318,* 222-244.

Barlow, H.B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology? *Perception. 1,* 371-394.

Baron, G., Stephan, H., & Frahm, H.D. (1987). Comparison of brain structure volumes in insecivora and primates: VI. Paleocortical components. *Journal of Hirnforsch, 28,* 463-477.

Baron-Cohen, S. (1991). Precursors to a theory of mind: understanding attention in others. In A. Whiten (Ed.), *Natural theories of mind.* (pp. 233-252). Oxford: Blackwell.

Baron-Cohen, S. (1994). How to build a baby that can read minds: Cognitive mechanisms in mindreading. *Cahiers de Psychologie Cognitive, 13,* 513-552.

Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind.* Cambridge, MA: The MIT Press.

Baron-Cohen, S., Cambell, R., Karmiloff-Smith, A., Grant, J., & Walker, J. (1995). Are children with autism blind to the mentalistic significance of the eyes? *British Journal of Developmental Psychology, 13,* 379-398.

Baron-Cohen, S., Cox, A., Baird, G., Swettenham, J., Nightingale, N., Morgan, K., Drew, A., & Charman, T. (1996). Psychological markers in the detection of autism in infancy in a large population. *British Journal of Psychiatry, 168,* 158-163.

Baron-Cohen, S., Leslie, A.M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition, 21,* 37-46.

Baron-Cohen, S. & Ring, H. (1994) A model of the mind-reading system: neuropsychological and neurobiological perspective. In: C, Lewis & P. Mitchell (Eds.), *Childrens early understanding of mind: origins and development.* (pp. 183-207), Hove: Erlbaum.

Baron-Cohen, S., Ring, H., Moriarty, J., Schmitz, B., Costa, D., & Ell, P. (1995). Recognition of mental state terms: clinical findings in children with autism, and a functional imaging study of normal adults. *British Journal of Psychiatry, 165,* 640-649.

Barton, R.A. (1996). Neocortex size and behavioural ecology. *Proceedings of the Royal Society London Biological Sciences, 263,* 173-177.

Barton, R.A., & Dunbar, R.I.M. (1997). Evolution of the social brain. In: A. Whiten & R.W. Byrne (Eds.), *Machiavellian intelligence 2: Evaluations and extensions.* Cambridge: Cambridge University Press (in press).

Barton, R.A., & Purvis, A. (1994). Primate brains and ecology: looking beneath the surface. In: J.R. Anderson, B. Thierry, & N. Herrenschmidt (Eds.), *Current primatology: Proceedings of the XIVth Congress of the International Primatological Society.* (pp. 1-11). Strasbourg: University of Strasbourg.

Barton, R.A., Purvis, A., & Harvey, P.H. (1995). Evolutionary radiation of visual and olfactory brain systems in primates, bats and insectivores. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 348,* 381-392.

Bauman, M.L. & Kemper, T. (1985). Histoanatomic observation of the brain in early infantile autism. *Neurology, 35,* 866-874.

Baylis, G.C., Rolls, E.T., & Leonard, C.M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex of the superior temporal sulcus of the macaque monkey. *Brain Research, 342,* 91-102.

Baylis, G.C., Rolls, E.T., & Leonard, C.M. (1987). Functional subdivisions of the temporal lobe neocortex. *Journal of Neuroscience, 7,* 330-342.

Beauregard, M., Malkova, L., & Bachevalier, J. (1995). Stereotypies and loss of social affiliation after early hippocampectomy in primates. *NeuroReport, 6,* 2521-2526.

Bernstein, I.S. (1981). Dominance: the baby and the bath water. *Behavioral and Brain Sciences, 4,* 419-457.

Bertrand, M. (1969). The behavioural repertoire of the stumptail macaque: a descriptive and comparative study. *Bibliotheca Primatologia, 11,* 1-273.

Blake, J., O'Rouke, P., & Borzelling, G. (1994). Form and function in the development of pointing and reaching gestures. *Infant Behavior & Development, 17,* 195-203.

Blaschke, M., & Ettlinger, G. (1987). Pointing as an act of social communication by monkeys. *Animal Behaviour, 35,* 1520-1523.

Blurton-Jones, N.B., & Trollope, J. (1968). Social behavior of stump-tailed macaques in captivity. *Primates, 9,* 365-394.

Bolwig, N. (1964). Facial expression in primates with remarks on a parallel development in certain carnivores (a preliminary report on work in progress). *Behaviour, 22,* 165-192.

Bolwig, N. (1978). Communicative signals and social behaviour of some African monkeys: a comparative study. *Primates, 19,* 61-99.

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience, 16,* 3737-3744.

Boussaoud, D., Ungerleider, L.G., & Desimone, R. (1990). Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. *Journal of Comparative Neurology, 296,* 462-495.

Boysen, S.T., & Bernston, G.G. (1989). Conspecific recognition in the chimpanzee (*Pan troglodytes*): cardiac responses to significant others. *Journal of Comparative Psychology, 103,* 215-220.

Boysen, S.T., & Berntson, G.G. (1986). Cardiac correlates of individual recognition in the chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology, 100,* 321-324.

Brammer, G.L., McGuire, M.T., & Raleigh, M.J. (1987). Similarity of 5-HT2 receptor sites in dominant and subordinate vervet monkeys. *Pharmacology, Biochemistry and Behavior, 27,* 701-705.

Breiter, H.C., Etcoff, N.L., Whalen, P.J., Kennedy, W.A., Rauch, S.L., Buckner, R.L., Strauss, M.M., Hyman, S., & Rosen, B. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron, 17,* 875-887.

Brody, E.B., & Rosvold, H.E. (1952). Influence of prefrontal lobotomy on social interaction in a monkey group. *Psychosomatic Medicine, 14,* 406-415.

Brothers, L. (1990). The social brain: a project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience, 1,* 27-51.

Brothers, L. (1992). Perception of social acts in primates:cognition and neurobiology. *Seminars in the Neurosciences, 4,* 409-414.

Brothers, L. (1994). Neurophysiology of the perception of intentions by primates. In M. Gazzaniga (Ed.), *The cognitive neurosciences.* (pp. 1107-1115). Massachusetts,USA: MIT Press.

Brothers, L. (1997). *Friday's footprint: How society shapes the human mind.* New York: Oxford University Press (in press).

Brothers, L., & Ring, B. (1992). A neuroethological framework for the representation of minds. *Journal of Cognitive Neuroscience, 4,* 107-118.

Brothers, L., & Ring, B. (1993). Medial temporal neurons in the macaque monkey with responses selective for aspects of social stimuli. *Behavioural Brain Research, 57,* 53-61.

Brothers, L., Ring, B., & Kling, A. (1990). Response of neurons in the macaque amygdala to complex social stimuli. *Behavioural Brain Research, 41,* 199-213.

Brown, S., & Shafer, E.A. (1888). An investigation into the functions of the occipital and temporal lobes of the monkey's brain. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 179,* 303-327.

Bruce, C. (1982). Face recognition by monkeys: absence of an inversion effect. *Neuropsychologia, 20,* 515-521.

Bruce, C., Desimone, R., & Gross, C.G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology, 46,* 369-384.

Bruce, V., Cowey, A., Ellis, A.W. & Perrett, D.I. (1992, Eds.). *Processing the facial image.* Oxford: Clarendon Press.

Bruce, V, & Green, P.R. (1990). *Visual perception: Physiology, psychology and ecology.* London: Lawrence Arlbaum Associates.

Bruce, V, & Young, A.W. (1986). Understanding face recognition. *British Jounal of Psychology, 77,* 305-327.

Bullier, J., Schall, J.D., & Morel, A. (1996). Functional streams in occipito-frontal connections in the monkey. *Behavioural Brain Research, 76,* 89-97.

Burger, J., Gochfeld, M., & Murray, B.G. (1992). Risk discrimination of eye contact and directness of approach in black iguanas (*Ctenosaura similis*). *Journal of Comparative Psychology, 106,* 97-101.

Burger, J., Gochfield, M., & Murray, B.G. (1991). Role of predator eye size in risk perception by basking black iguanas (*Ctenosaura similis*). *Animal Behaviour, 42,* 471-476.

Burghardt, G.M. (1990). Cognitive ethology and critical anthropomorphism: a snake with two heads and hog-nosed snakes that play dead. In: C.A. Ristau (Ed.), *Cognitive ethology: The minds of other animals.* Hillside, NJ: Lawrence Erlbaum.

Butter, C.M., Mishkin, M., & Mirsky, A.F. (1968). Emotional responses toward humans in monkeys with selective frontal lesions. *Physiology and Behaviour, 3,* 213-215.

Butterworth, G. (1991). The ontogeny and phylogeny of joint visual attention. In: A. Whiten (Ed.), *Natural theories of mind.* (pp. 223-232). Oxford: Blackwell.

Butterworth, G., & Cochran, E. (1980). Towards a mechanism of joint visual attention in human infancy. *International Journal of Behavioral Development, 3,* 253-272.

Butterworth, G., & Jarrett, N. (1991). What minds have in common is space: spatial mechanisms serving joint visual attention in infancy. *British Journal of Developmental Psychology, 9,* 55-72.

Byrne, R.W. (1995a). *The thinking ape: Evolutionary origins of intelligence.* Oxford: Oxford University Press.

Byrne, R.W. (1995b). Primate cognition: comparing problems and skills. *American Journal of Primatology, 37,* 127-141.

Byrne, R.W. (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In A. Whiten & R.W. Byrne (Eds.), *Machiavellian intelligence 2: Evaluations and extensions.* Cambridge: Cambridge University Press.

Byrne, R.W., & Byrne, J.M.E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): variability and standardization. *American Journal of Primatology, 31,* 241-261.

Byrne, R.W., & Russon, A.E. (1997). Learning by imitation: a hierarchical approach. *Behavioural and Brain Sciences,* (in press)

Byrne, R.W., & Whiten, A. (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans.* Oxford: Oxford University Press.

Calder, A.J., Young, A.W., Rowland, D., Perrett, D.I., Hodges, J.R., & Etcoff, N.L. (1996). Facial emotion recognition after bilateral amygdala damage: differentially severe impairment of fear. *Cognitive Neuropsychology, 13,* 699-745.

Call, J., & Tomasello, M. (1994a). The social learning of tool use by orangutans (*Pongo pygmaeus*). *Human Evolution, 9,* 297-313.

Call, J., & Tomasello, M. (1994b). Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 108,* 307-317.

Camaioni, L., Perucchini, P., Muratori, F., Milone, A., & Siri, R. (1994). A longitudinal examination of the communicative gestures deficit in young aytistic children. Paper presented at the symposium "Social and communicative aspects of young autistic children's development", IX Biennial meeting of the *International Society for Infant Study*, Paris.

Cambell, R., Heywood, C.A., Cowey, A., Regard, M., & Landis, T. (1990). Sensitivity to eye gaze in prosopagnosic patients and monkeys with superior temporal sulcus ablation. *Neuropsychologia, 28,* 1123-1142.

Carey, D.P. (1996). "Monkey see, monkey do" cells. *Current Biology, 6,* 1087-1089.

Carlson, N. R. (1986). *Physiology of behavior.* Boston: Allyn and Bacon, Inc.

Carmichael, S.T., Clugnet, M.C., & Price, J.L. (1994). Central olfactory connections in the macaque monkey. *Journal of Comparative Neurology, 346,* 403-434.

Carmichael, S.T., & Price, J.L. (1995). Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys. *Journal of Comparative Neurology, 363,* 615-641.

Carpenter, M., Tomasello, M., & Savage-Rumbaugh, S. (1995). Joint attention and imitative learning in children, chimpanzees and encultured chimpanzees. *Social Development, 4,* 217-237.

Cavada, C., & Goldman-Rakic, P.S. (1989). Posterior parietal cortex in rhesus monkey II: evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *Journal of Comparative Neurology, 287,* 422-445.

Cavada, C., & Goldman-Rakic, P.S. (1989). Posterior parietal cortex in rhesus monkey I: parcellation of areas based on distictive limbic and sensory corticocortical connections. *Journal of Comparative Neurology, 287,* 393-421.

Chance, M.R.A. (1967). Attention structure as a basis of primate rank orders. *Man, 2,* 503-518.

Cheney, D.L., & Seyfarth, R.M. (1982) Recognition of individuals within and between groups of free-ranging vervet monkeys. *Am. Zool., 22,* 519-529.

Cheney, D.L., & Seyfarth, R.M. (1985a). Social and non-social knowledge in vervet monkeys. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 308,* 187-201.

Cheney, D.L., & Seyfarth, R.M. (1985b) Vervet monkey alarm calls: Manipulation through shared information. *Behaviour, 93,* 150-166.

Cheney, D.L., & Seyfarth, R.M. (1986). The recognition of social alliances by vervet monkeys. *Animal Behaviour, 34,* 1722-1731.

Cheney, D.L., & Seyfarth, R.M. (1988). Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour, 36,* 477-486.

Cheney, D.L., & Seyfarth, R.M. (1990a). Attending to behaviour versus attending to knowledge: examining monkey's attribution of mental states. *Animal Behaviour, 40,* 742-753.

Cheney, D.L., & Seyfarth, R.M. (1990b). The representation of social relations by monkeys. *Cognition, 37,* 167-196.

Cheney, D.L., & Seyfarth, R.M. (1990c). *How monkeys see the world: Inside the mind of another species.* Chicago: University of Chicago Press.

Cheney, D.L., & Seyfarth, R.M. (1991). Reading minds or reading behaviour? Tests for a theory of mind in monkeys. In A. Whiten (Ed.), *Natural theories of mind.* (pp. 175-194). Oxford: Blackwell.

Cheney, D.L., & Seyfarth, R.M. (1996). Function and intention in the calls of non-human primates. *Proceedings of the British Academy, 88,* 59-76.

Cheney, D.L., Seyfarth, R.M., & Smuts, B. (1986). Social relationships and social cognition in nonhuman primates. *Science, 234,* 1361-1366.

Chomsky, N. (1967). The general properties of language. In: F.L. Darley (Ed.), *Brain mechanisms underlying speech and language.* (pp. 73-88). New York: Grune & Stratton.

Clutton-Brock, T.H., & Harvey, P.H. (1977). Primate ecology and social organization. *Journal of Zoology, 183,* 1-39.

Coss, R.G. (1978). Perceptual determinants of gaze aversion by the lesser mouse lemur (*Microcerbus murinus*). The role of two facing eyes. *Behaviour, 64,* 248-267.

Courchesne, E. (1997). Brainstem, cerebellar and limbic neuroanatomical abnormalities in autism. *Current Opinion in Neurobiology, 7,* 269-278.

Courchesne, E., Townsend, J., Asknoomoff, N.A., Saitoh, O., Yeung-Courchesne, R., Lincoln, A.J., James, H.E., Haas, R.H., Schreibman, L., & Lau, L. (1994). Impairment in shifting attention in autistic and cerebellar patients. *Behavioural Neuroscience, 108,* 848-865.

Coussi-Korbel, S. (1994). Learning to outwit a competitor in mangabeys (*Cercocbus torquatus torquatus*). *Journal of Comparative Psychology, 108,* 164-171.

Crosby, E.C., & Humphrey, T. (1941). Studies of the vertebrate telencephalon. II: The nuclear pattern of the anterior olfactory nucleus, tuberculum olfactorium and the amygdaloid complex in adult man. *Journal of Comparative Neurology, 74,* 309-352.

Crosby, E.C., & Humphrey, T. (1944). Studies of the vertebrate telencephalon. III: The amygdaloid complex in the shrew (*Blarina brevicauda*). *Journal of Comparative Neurology, 81,* 285-305.

Cusick, C.G., Seltzer, B., Cola, M., & Griggs, E. (1995). Chemoarchitectonics and corticocortical terminations within the superior temporal sulcus of the rhesus monkey: Evidence for subdivisions of superior temporal polysensory cortex. *Journal of Comparative Neurology, 360,* 513-535.

Custance, D.M., Whiten, A., & Bard, K.A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitary actions-Hayes and Hayes (1952) revisited. *Behaviour, 132,* 837-859.

D'Amato, M.R., & Van Sant, P. (1988). The person concept in monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes, 14,* 43-55.

Damasio, A.R. (1985). Prosopagnosia. *Trends In Neurosciences, 8,* 132-135.

Damasio, A.R. (1990). Category-related recognition defects as a clue to the neural substrates of knowledge. *Trends In Neurosciences, 13,* 95-98.

Damasio, A.R. (1994). *Descartes' error: Emotion, reason and the human brain.* London: Picador.

Damasio, A.R., Damasio, H. & Christen, Y. (1996, Eds.). *Neurobiology of decision-making.* Berlin: Springer.

Damasio, A.R. & Maurer, R.G. (1978). A neurological model for childhood autism. *Archives of Neurology, 35,* 777-786.

Damasio, A.R., Tranel, D., & Damasio, H. (1990). Individuals with sociopathic behavior caused by frontal damage fail to respond automatically to social stimuli. *Behavioural Brain Research, 41,* 81-94.

Damasio, H., Grabowski, T., Frank, R., Galaburda, A.M., & Damasio, A.R. (1994). The return of Phileas Gage: clues about the brain from the skull of a famous patient. *Science, 264,* 1102-1105.

Dasser, V. (1987). Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology, 76,* 65-73.

Dasser, V. (1988). A social concept in Java monkeys. *Animal Behaviour, 36,* 225-230.

Davies, S., Bishop, D., Manstead, A.S.R., & Tantam, D. (1994). Face perception in children with autism and Asberger's syndrome. *Journal of Child Psychology and Psychiatry, 35,* 1033-1057.

Dawkins, R. (1981). Communication. In: D. McFarland (Ed.), *The Oxford companion to animal behaviour.* (pp. 78-91), Oxford: Oxford University Press.

de Waal, F.B.M. (1982). *Chimpanzee politics: Power and sex among the apes.* Baltimore: John Hopkins University Press.

de Waal, F.B.M. (1989). *Peacemaking among primates.* Cambridge, MA: Harvard University Press.

de Waal, F.B.M. (1987). Dynamics of social relationships. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies.* (pp. 421-430). Chicago: University of Chicago Press.

Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary,B., Woods, R., Mazziotta, J.C., & Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature, 371.* 600-602.

Deets, A.C., Harlow, H.F., Singh, S.D., & Blomquist, A.J. (1970). Effects of bilateral lesions of the frontal granular cortex on the social behaviour of rhesus monkeys. *Journal of Comparative and Physiological Psychology, 72.* 452-461.

Delson, E. (1980). Fossil macaques, phyletic relationships and a scenario of deployment. In: D.G. Lindburg (Ed.), *The macaques: Studies in ecology, behavior and evolution.* (pp. 10-30). New York: Van Nostrand Reinhold.

Demaria, C., & Thierry, B. (1988). Responses to animal stimulus photographs in stumptailed macaques (*Macaca arctoides*). *Primates, 29,* 237-244.

Dennett, D.C. (1983). Intentional systems in cognitive ethology: the "Panglosian Paradigm" defended. *Behavioral and Brain Sciences, 6,* 343-390.

Dennett, D.C. (1987). *The intentional stance.* Cambridge, MA: The MIT Press.

Desimone, R., Albright, T.D., Gross, C.G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience, 4,* 2051-2062.

Desimone, R., & Ungerleider, L.G. (1986). Multiple visual areas in the caudal superior temporal sulcus of the macaque. *Journal of Comparative Neurology, 248,* 164-189.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V, & Rizzolatti, G. (1992). Understanding motor events:a neurophysiological study. *Experimental Brain Research, 91,* 176-180.

Dicks, D., Myers, R.E., & Kling. A. (1969). Uncus and amygdala lesions: effects on social behavior in the free ranging rhesus monkey. *Science, 165,* 69-71.

Dittrich, W. (1990). Representation of faces in long-tailed macaques (*Macaca fascicularis*). *Ethology, 85,* 265-278.

Dittrich, W. (1994). How monkeys see others: discrimination and recognition of monkey's shape. *Behavioural Processes, 33,* 139-154.

Downer, J.L. (1961). Changes in visual gnostic functions and emotional behaviour following unilateral temporal pole damage in the 'split-brain' monkey. *Nature, 191,* 50-51.

Dunbar, R.I.M. (1988). *Primate social systems.* London,UK: Croom Helm.

Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. *Folia Primatologia, 57,* 121-131.

Dunbar, R.I.M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution, 20,* 469-493.

Dunbar, R.I.M. (1995). Neocortex size and group size in primates: a test of the hypothesis. *Journal of Human Evolution, 28,* 287-296.

Dunbar, R.I.M. (1996). Determinants of group size in primates: a general model. *Proceedings of the British Academy, 88,* 33-57.

Dunbar, R.I.M., & Bever, J. (1997). Neocortex size determines group size in insectivores and carnivores. *Brain, Behavior and Evolution,* (in review).

Dunbar, R.I.M., & Joffe, T. (1997). Neocortex size determines social group size in prosimians. *Behaviour,* (in review).

Eacott, M.J., Heywood, C.A., Gross, C.G., & Cowey, A. (1993). Visual discrimination impairments following lesions of the superior temporal sulcus are not specific for facial stimuli. *Neuropsychologia, 31(6),* 609-619.

Eslinger, P.J., & Damasio, A.R. (1985). Severe disturbances of higher cognition after bilateral frontal lobe ablation: Patient EVR. *Neurology, 35,* 1731-1741.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology, 73,* 2608-2611.

Fairbanks, L. (1975). Communication of food quality in captive *Mcaca nemestrina* and free-ranging *Ateles geoffroyi*. *Primates, 16,* 181-190.

Falk, D. (1990). Brain evolution in *Homo*: the "radiator" theory. *Behavioral and Brain Sciences, 13,* 333-381.

Falk, D. (1992). *Braindance: New discoveries about human brain evolution.* New York: Henry Holt and Co.

Farah, M.J., McMullen, P.A., & Meyer, M.M. (1991). Can recognition of living things be selectively impaired? *Neuropsychologia, 29,* 185-193.

Farah, M.J., Meyer, M.M., & McCullen, P.A. (1996). The living/non-living dissociation is not an artifact: giving an a priori implausible hypothesis a strong test. *Cognitive Neuropsychology, 15,* 137-154.

Felleman, D.J., & Van Essen, D.C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1,* 1-47.

Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist, 125,* 1-15.

Finlay, B.L., & Darlington, R.B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science, 268,* 1578-1583.

Fletcher, D.J.C., & Michener, C.D. (1987, Eds.). *Kin recognition in animals.* Chicester: John Wiley and Sons.

Fletcher, P.C., Happe, F., Frith, U., Baker, S.C., Dolan, R.J., Frackowiak, R.S.J., & Frith, C.D. (1995). Other minds in the brain-a functional imaging study of theory of mind in story comprehension. *Cognition, 57,* 109-128.

Fletemeyer, J.R. (1978). Communication about potentially harmful foods in free-ranging Chacma baboons, *Papio ursinus.*. *Primates, 19,* 223-226.

Franzen, E.A., & Myers, R.E. (1973). Neural control of social behavior: prefrontal and anterior temporal cortex. *Neuropsychologia, 11,* 141-157.

Frederickson, W.T., & Sackett, G.P. (1984). Kin preferences in primates (*Macaca nemestrina*): relatedness or familiarity? *Journal of Comparative Psychology, 98,* 29-34.

Friedman, D.P., Murray, E.A., O'Neill, B., & Mishkin, M. (1986). Cortical connections of the somatosensory fields of the lateral sulcus of macaques: evidence for a corticolimbic pathway for touch. *Journal of Comparative Neurology, 252,* 323-347.

Fujita, K. (1990). Species preference by infant macaques with controlled social experience. *International Journal of Primatology, 11,* 553-573.

Fujita, K. (1993a). Development of visual preference for closely related species by infant and juvenile macaques with restricted social experience. *Primates, 34,* 141-150.

Fujita, K. (1993b). Role of some physical characteristics in species recognition by pigtail monkeys. *Primates, 34,* 133-140.

Fujita, K., & Watanabe, K. (1995). Visual preference for closely related species by Sulawesi macaques. *American Journal of Primatology, 37,* 253-261.

Funnell, E. & Sheridan, J. (1992). Categories of knowledge? Unfamiliar aspects of living and non-living things. *Cognitive Neuropsychology, 9,* 135-154.

Fuster, J.M. (1996). Frontal lobe and the cognitive foundation of behavioural action. In: A.R. Damasio, H. Damasio, & Y. Christen (Eds.), *Neurobiology of decision-making.* (pp. 47-62). Berlin: Springer Verlag.

Gaffan, D. (1994a). Role of the amygdala in picture discrimination learning with 24-hr intertrial intervals. *Experimental Brain Research, 99,* 423-430.

Gaffan, D. (1994b). Dissociated effects of perirhinal cortex ablation, fornix transection and amygdalectomy: evidence for multiple memory systems in the primate temporal lobe. *Experimental Brain Research, 99,* 411-422.

Gaffan, D. (1995) The monkey amygdala: current hypotheses of function. Paper presented at the *Meeting of European Neuroscience, Amsterdam.*

Gaffan, D., & Harrison, S. (1987). Amygdalectomy and disconnection in visual learning for auditory secondary reinforcement by monkeys. *Journal of Neuroscience, 7,* 2285-2292.

Gaffan, D., & Heywood, C.A. (1993). A spurious category-specific visual agnosia for living things in normal human and nonhuman primates. *Journal of Cognitive Neuroscience, 5,* 118-128.

Gaffan, D., & Murray, E.A. (1990). Amygdalar interaction with the mediodorsal nucleus of the thalamus and the ventromedial prefrontal cortex in stimulus-reward associative learning in the monkey. *Journal of Neuroscience, 10,* 3479-3493.

Gaffan, D., Murray, E.A., & Fabre-Thorpe, M. (1993). Interaction of the amygdala with the frontal lobe in reward memory. *European Journal of Neuroscience, 5,* 968-975.

Gaffan, E.A., Gaffan, D., & Harrison, S. (1988). Disconnection of the amygdala from visual association cortex impairs visual reward-association learning in monkeys. *Journal of Neuroscience, 8,* 3144-3150.

Galdikas, B.M.F. (1995). *Reflections of Eden: My years with the orangutans of Borneo.* Boston: Little, Brown and Co.

Galaburda, A.M., & Pandya, D.N. (1983). The intrinsic architectonic and connectional organization of the superior temporal region of the rhesus monkey. *Journal of Comparative Neurology, 221,* 169-184.

Gallese, V, Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain, 119,* 593-609.

Gallup, G.G.(1970). Chimpanzees: Self-recognition. *Science, 167,* 86-87.

Gallup, G.G. (1982). Self-awareness and the emergence of mind in primates. *American Journal of Primatology, 2,* 237-248.

Gallup, G.G., Cummings, W.H., & Nash, R.F. (1972). The experimenter as an independent variable in studies of animal hypnosis in chickens (*Gallus gallus*). *Animal Behaviour, 20,* 166-169.

Gautier, J.-P., & Gautier, A. (1977). Communication in Old World monkeys. In: T.A. Sebeok (Ed.), *How animals communicate.* (pp. 890-964). Bloomington: Indiana University Press.

Ghika-Schmid, F., Assal, G., De Tribolet, N., & Regli, F. (1995). Kluver-Bucy syndrome after left anterior temporal resection. *Neuropsychologia, 33,* 101-113.

Gibson, K.R. (1986). Cognition, brain size and the extraction of embedded food resources. In: J. Else & P.C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour.* (pp. 93-105). Cambridge: Cambridge University Press.

Goel, V, Grafman, J., Sadato, N., & Hallett, M. (1995). Modelling other minds. *NeuroReport, 6,* 1741-1746.

Goldman-Rakic, P.S. (1987). Circuitry of primate prefrontal cortex and regulation of behaviour by representational memory. In: F. Plum & V. Mountcastle, V (Eds.), *Handbook of physiology: The nervous system.* (pp. 373-417). Bethesda, USA: American Physiology Society.

Gomez, J.C. (1990). The emergence of intentional communication as a problem-solving strategy in the gorilla. In: S.T. Parker & K.R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: comparative developmental approaches.* (pp. 333-355). Cambridge: Cambridge University press.

Gomez, J.C. (1991). Visual behaviour as a window for reading the mind of others in primates. In: A. Whiten (Ed.), *Natural theories of mind.* (pp. 195-208). Oxford: Blackwell.

Gomez, J.C. (1996). Ostensive behavior in great apes: the role of eye contact. In A.E. Russon, S.T. Parker, & K.A. Bard (Eds.), *Reaching into thought.* (pp. 131-151). Cambridge: Cambridge University Press.

Good, P.F., & Morrison, J.H. (1995). Morphology and kainate-receptor immunoreactivity of identified neurons within the entorhianl cortex projecting to superior temporal sulcus in the cynomolgus monkey. *Journal of Comparative Neurology, 357,* 25-35.

Goodale, M., & Milner, A.D. (1992) Separate visual pathways for perception and action. *Trends in Neurosciences, 15,* 20-25.

Gouzoules, S. & Gouzoules, H. (1987) Kinship. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, &. T.T. Struhsaker (Eds.) *Primate societies,* (pp. 299-305), Chicago: University of Chicago Press.

Griffin, D.R. (1978). Prospects for a cognitive ethology. *Behavioral and Brain Sciences, 4,* 527-538.

Gross, C.G., Rocha-Miranda, C.E., & Bender, D.B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology, 35,* 96-111.

Haith, M.M., Bergman, T., & Moore, M.J. (1977). Eye contact and face scanning in early infancy. *Science, 198,* 853-855.

Hall, K.R.L. (1963). Observational learning in monkeys and apes. *British Journal of Psychology, 54,* 201-226.

Hamann, S.B., Stefanacci, L., Squire, L.R., Adolphs, R., Tranel, D., Damasio, H., & Damasio, A.R. (1996). Recognising facial emotion. *Nature, 379,* 497

Hampton, R.R. (1994). Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). *Behaviour, 130,* 41-51.

Harre, R. & Reynolds, V. (1984, Eds.). *The meaning of primate signals.* Cambridge: Cambridge University Press.

Harlow, H.F. (1958). The nature of love. *American Psychologist, 13,* 673-685.

Harrison, K. (1996). *Skills used in food processing by vervet monkeys* (*Cercopithecus aethiops*). Unpublished Doctoral Thesis, University of St Andrews.

Harvey, P.H., & Pagel, M.D. (1991). *The comparative method in evolutionary biology.* Oxford: Oxford University Press.

Hasselmo, M.E., Rolls, E.T., Baylis, G.C., & Nalwa, V. (1989). Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. *Experimental Brain Research, 75,* 417-429.

Hasselmo, M.E., Rolls, E.T., & Bayliss, G.C. (1989). The role of expression and identity in the face selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research, 32,* 203-218.

Hauser, M.D. (1996). *The evolution of communication.* Cambridge, MA: MIT Press.

Hauser, M.D., Kralik, J., Botto-Mahan, C., Garrett, M., & Oser, J. (1995). Self-recognition in primates: Phylogeny and the salience of species-typical features. *Proceedings of the National Academy of Sciences USA, 92,* 10811-10814.

Hayes, K.J. & Hayes, C. (1952). Imitation in a home-reared chimpanzee. *Journal of Comparative and Physiological Psychology, 45,* 450-459.

Hennig, C.W. (1977). Effect of simulated predation on tonic immobility in *Anolis carolinensis*: The role of eye contact. *Bulletin of the Psychonomic Society, 9,* 239-242.

Herzog,A.G., & Van Hoesen, G.W. (1976). Temporal neocortical afferent connections to the amygdala in the rhesus monkey. *Brain Research, 115,* 57-69.

Hess, J., Novak, M.A., & Povinelli, D.J. (1993). 'Natural pointing' in a rhesus monkey, but no evidence of empathy. *Animal Behaviour, 46,* 1023-1025.

Hetzler, B.E., & Griffin, J.L. (1981). Infantile autism and the temporal lobe of the brain. *Journal of Autism and Developmental Disorders, 11,* 317-330.

Heyes, C.M. (1993). Anecdotes, training, trapping and triangulating: do animals attribute mental states? *Animal Behaviour, 46,* 177-188.

Heyes, C.M. (1997). Theory of mind in nonhuman primates. *Behavioral and Brain Sciences,* (in press).

Heywood, C.A., & Cowey, A. (1992). The role of the "face-cell" area in the discrimination and recognition of faces by monkeys. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 335,* 31-38.

Hietanen, J.K., Perrett, D.I., Oram, M.W., Benson, P.J., & Dittrich, W.H. (1992). The effects of lighting conditions on responses of cells selective for face views in the macaque temporal cortex. *Experimental Brain Research, 89,* 157-171.

Hikosaka, K., Iwai, E., Saito, H., & Tanaka, K. (1988). Polysensory properties of neurons in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. *Journal of Neurophysiology, 60,* 1615-1637.

Hikosaka, K., Matsuto, T., Sakai, S., & Iwai, E. (1990). Three regions in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. In: E. Iwai and M. Mishkin (Eds.) *Vision, memory and the temporal lobe.* (pp. 347-353). New York: Elsevier Science Publishing Co., Inc.

Hildreth, & Koch, C. (1987). The analysis of visual motion: From computational theory to neuronal mechanisms. *Annual Review of Neuroscience, 10,* 477-533.

Hinde, R.A., & Rowell, T.E. (1961). Communication by postures and facial expression in the rhesus monkey (*Macaca mulatta*). *Symposium of the Zoological Society of London, 8,* 1-21.

Hirstein, W., & Ramachandran, V.S. (1997). Capgras syndrome: a novel probe for understanding the neural representation of the identity and familiarity of persons. *Proceedings of the Royal Society of London: Biological Sciences, 264,* 437-444.

Hobson, R.P. (1986). The autistic child's appraisal of expressions of emotion. *Journal of Child Psychology and Psychiatry, 27,* 321-342.

Hobson, R.P., Ouston, J., & Lee, A. (1988). What's in a face? The case of autism. *British Journal of Psychology, 79,* 441-453.

Holloway, R.L. (1966). Cranial capacity, neural reorganization and hominid evolution: a search for more suitable parameters. *American Anthropologist, 68,* 103-121.

Horel, J.A., & Keating, E.G. (1969). Partial Kluver-Bucy syndrome produced by cortical disconnection. *Brain Research, 16,* 281-284.

Horel, J.A., & Keating, E.G. (1972). Recovery from a partial Kluver-Bucy syndrome in the monkey produced by disconnection. *Journal of Comparative and Physiological Psychology, 79,* 105-114.

Horel, J.A., Keating, E.G., & Misantone, L.J. (1975). Partial Kluver-Bucy syndrome produced by destroying temporal neocortex or amygdala. *Brain Research, 94,* 347-359.

Horel, J.A., & Misantone, L.J. (1974). The Kluver-Bucy syndrome produced by partial isolation of the temporal lobe. *Experimental Neurology, 42,* 101-112.

Hornak, J., Rolls, E.T., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia, 34,* 247-261.

Hubel, D.H. & Wiesel, T.N. (1968) Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, 195,* 215-243.

Huber, E. (1931). *Evolution of facial musculature and facial expression.* Baltimore: John Hopkins Press.

Huber, E. (1961). The facial musculature and its innervation. In: C.G. Hartman & W.L. Straus (Eds.), *Anatomy of the rhesus monkey (Macaca mulatta).* (pp. 176-188). New York: Hafner.

Huffman, M.A. (1996). Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In: C.M. Heyes & B.G. Galef (Eds.), *Social learning in animals: The roots of culture.* (pp. 267-289). San Diego, CA: Academic Press Inc.

Humphrey, N.K. (1974). Species and individuals in the perceptual world of monkeys. *Perception, 3,* 105-114.

Humphrey, N.K. (1976). The social function of intellect. In: P.P.G. Bateson & R.A. Hinde (Eds.), *Growing points in ethology.* (pp. 303-317). Cambridge: Cambridge University Press.

Insausti,R., Amaral, D.G., & Cowan, W.M. (1987). The entorhinal cortex: III. Subcortical afferents. *Journal of Comparative Neurology, 264,* 396-408.

Itakura, S. (1996). An exploratory study of gaze-monitoring in non-human primates. *Japanese Psychological Research, 38,* 174-180.

Itakura, S., & Anderson, J.R. (1996). Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Cahiers de Psychologie Cognitive, 15,* 103-112.

Itakura, S., & Tanaka, M. (1997). Use of experimenter-given cues during object-choice tasks by chimpanzees (*Pan troglodytes*), an orangutan (*Pongo pygmaeus*), and human infants (*Homo sapiens*). *Journal of Comparative Psychology.* (in press).

Iwai, E., & Yukie, M. (1987). Amygdalofugal and amygdalopetal connections with modality-specific visual cortical areas in macaques (*Macaca fuscata, M.mulatta,* and *M.fascicularis*). *Journal of Comparative Neurology, 261,* 362-387.

Iwai, E., Yukie, M., Suyama, H., & Shirakawa, S. (1987). Amygdalar connections with middle and inferior temporal gyri of the monkey. *Neuroscience Letters, 83,* 25-29.

Jacobson, R. (1986). Disorders of facial recognition, social behaviour and affect after combined bilateral amygdalotomy and subcaudate tractotomy-a clinical and experimental study. *Psychological Medicine, 16,* 439-450.

Jacobson, S., & Trojanowski, J.Q. (1975). Amygdaloid projections to prefrontal granular cortex in rhesus monkey demonstrated with horseradish peroxidase. *Brain Research, 100,* 132-139.

Jeannerod, M., Arbib, M.A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: the cortical mechanisms of visuomotor transformations. *Trends In Neurosciences, 18,* 314-320.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception and Psychophysics, 14,* 201-211.

Johnson, M.H. & Morton, J. (1991). *Biology and cognitive development: The case of face recognition.* Oxford: Blackwell.

Johnston, J.B. (1923). Further contributions to the study of the evolution of the forebrain. *Journal of Comparative Neurology, 35,* 337-481.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science, 153,* 501-507.

Jolly, A. (1972). *The evolution of primate behavior.* First edition. New York: Macmillan.

Jolly, A. (1985). *The evolution of primate behavior.* Second edition. New York: Macmillan.

Jones, E.G., & Burton, H. (1976). A projection from the medial pulvinar to the amygdala in primates. *Brain Research, 104,* 142-147.

Jones, E.G., Burton, H., Saper, C.B., & Swanson, L.W. (1975). Midbrain, diencephalic and cortical relationships of the basal nucleus of meynert and associated structures in primates. *Journal of Comparative Neurology, 167,* 385-420.

Jones, E.G., & Powell, T.P.S. (1970). An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. *Brain, 93,* 793-820.

Jurgens, U. (1982). Amygdalar vocalization pathways in the squirrel monkey. *Brain Research, 241.* 189-196.

Kanazawa, S. (1996). Recognition of facial expressions in a japanese monkey (*Macaca fuscata*) and humans (*Homo sapiens*). *Primates, 37,* 25-38.

Kanner, L. (1943). Autistic disturbance of affective contact. *Nervous Child, 2,* 217-250.

Kaplan, G., & Rogers, L.J. (1996). Gaze direction and visual attention in orangutans. *Joint Congress of the International Primatological Society and Americal Society of Primatologists, 273,* (abstract)

Karadi, Z., Oomura, Y., Nishino, H., & Aou, S. (1989). Olfactory coding in the monkey lateral hypothalamus- behavioral and neurochemical propoerties of odor-responding neurons. *Physiology and Behaviour, 45,* 1249-1257.

Kawai, I. (1966). Changes in social behavior following bilateral removal of the posterior parts of the superior temporal gyri in Japanese monkeys. *Primates, 7,* 1-20.

Keating, C.F., & Keating, E.G. (1982). Visual scan patterns of rhesus monkeys viewing faces. *Perception, 11,* 211-219.

Keating, C.F., & Keating, E.G. (1993). Monkeys and mug shots: cues used by rhesus monkeys (*Macaca mulatta*) to recognise a human face. *Journal of Comparative Psychology, 107,* 131-139.

Kemp, R., McManus, C., & Pigott, T. (1990). Sensitivity to the displacement of facial features in negative and inverted images. *Perception, 19,* 531-543.

Kendrick, K.M. (1994). Neurobiological correlates of visual and olfactory recognition in sheep. *Behavioural Processes, 33,* 89-112.

Kendrick, K.M., & Baldwin, B.A. (1987). Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. *Science, 236,* 448-450.

King, B.J. (1986). Extractive foraging and the evolution of primate intelligence. *Human Evolution, 1,* 361-372.

Kingdon, J.S. (1980). The role of visual signals and face patterns in African forest monkeys (guenons) of the genus *Cercopithecus. Transactions of the Zoological Society of London, 35,* 425-475.

Kling, A. (1966). Ontogenetic and phylogenetic studies on the amygdaloid complex. *Psychosomatic Medicine, 28,* 155-161.

Kling, A. (1968). Effects of amygdalectomy and testosterone on sexual behavior of male juvenille macaques. *Journal of Comparative and Physiological Psychology, 65,* 466-471.

Kling, A. (1974). Differential effects of amygdalectomy in male and female nonhuman primates. *Archives of Sexual Behavior, 3,* 129-134.

Kling, A. (1981). Influence of temporal lobe lesions on radio-telemetered electrical activity of amygdala to social stimuli in monkey. In Y. Ben-Ari (Ed.), *The amygdaloid complex: Inserm symposium 20.* (pp. 271-280). Amsterdam: Elsevier/North Holland.

Kling, A. & Carpenter, R. (1968). Amygdalectomy and social behavior in a caged-group of vervets (*C. aethiops*). *Proceedings of the Second International Congress of Primatology.* (Pp. 232), New York: Karger

Kling, A., & Cornell, R. (1971). Amygdalectomy and social behaviour in the caged stump-tailed macaque. *Folia Primatologia, 14,* 91-103.

Kling, A. & Dunne, K. (1976). Socio-environmental factors affecting behavior and plasma testosterone in normal and amygdala lesioned *M. Speciosa. Primates, 17,* 23-42.

Kling, A., & Green, P.C. (1967). Effects of neonatal amygdalectomy in the maternally reared and maternally deprived macaque. *Nature, 213,* 742-743.

Kling, A., Lancaster, J., & Benitone, J. (1970). Amygdalectomy in the free-ranging vervet. *Journal of Psychiatric Research, 7,* 191-199.

Kling, A., & Steklis, H.D. (1976). A neural substrate for affiliative behaviour in non-human primates. *Brain, Behavior and Evolution, 13,* 216-238.

Kling, A., Steklis, H.D., & Deutsch, S. (1979). Radiotelemetered activity from the amygdala during social interactions in the monkey. *Experimental Neurology, 66,* 88-96.

Kling, A.S., & Brothers, L. (1991). The amygdala and social behaviour. In: J.P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory and mental dysfunction.* (pp. 353-378). New York: Wiley-Liss.

Kling, A.S., Lloyd, R.L., & Perryman, K.M. (1987). Slow wave changes in amygdala to visual, auditory and social stimuli following lesions of the inferior temporal cortex in squirrel monkey (*Saimiri sciureus*). *Behavioural and Neural Biology, 47,* 54-72.

Kluver, H., & Bucy, P.C. (1937). "Psychic blindness" and other symptoms following bilateral temporal lobectomy in rhesus monkeys. *American Journal of Physiology, 119,* 352-353.

Kluver, H., & Bucy, P.C. (1938). An analysis of certain effects of bilateral temporal lobectomy in the rhesus monkey, with special reference to "psychic blindness". *Journal of Psychology, 5,* 33-54.

Kluver, H., & Bucy, P.C. (1939). Preliminary analysis of functions of the temporal lobes in monkeys. *Archives of Neurology and Psychiatry, 42,* 979-1000.

Kobatake, E., & Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *Journal of Neurophysiology, 71(3),* 856-867.

Kobayashi, H. & Kohshima, S. (1997). Morphological uniqueness of human eyes and its adaptive meaning. *Nature,* (in press).

Kohler, W. (1925). *The mentality of apes.* London: Routledge and Kegan Paul.

Komatsu, H., & Ideura, Y. (1993). Relationships between color, shape, and patterns selectivities of neurons in the inferior temporal cortex of the monkey. *Journal of Neurophysiology, 70,* 677-694.

Kordower, J.H., Piecinski, P., & Rakic, P. (1992). Neurogenesis of the amygdaloid nuclear complex in the Rhesus monkey. *Developmental Brain Research, 68,* 9-15.

Krebs, J.R. & Dawkins, R. (1984). Animal signals: mind reading and manipulation. In: J.R. Krebs & R. Dawkins (Eds.) *Behavioural ecology: an evolutionary approach,* (pp. 380-401). Oxford: Blackwell.

Kudo, H., Lowen, S. & Dunbar, R.I.M. (1997). Neocortex size determines clique size in primates. *Behaviour,* (in review).

Kummer, H. (1967). Tripartite relations in hamadryas baboons. In: S. Altmann (Ed.) *Social communication among primates.* (pp. 63-71), Chicago: University of Chicago Press.

Kummer, H. (1968). Social organization of hamadryas baboons: A field study. *Bibliotheca Primatologia, 6,* 1-189.

Kummer, H. (1995). *In quest of the sacred baboon.: A scientist's journey.* Princeton: Princeton University Press.

Kummer, H., Anzenberger, G., & Hemlrijk, C.K. (1996). Hiding and perspective-taking in long-tailed macaques (*Macaca fascicularis*). *Journal of Comparative Psychology, 110,* 97-102.

Kyes, R.C., & Candland, D.K. (1987). Baboon (*Papio hamadryas*) visual preferences for regions of the face. *Journal of Comparative Psychology, 101,* 345-348.

Kyes, R.C., Mayer, E., & Bunnell, B.N. (1992). Perception of stimuli presented as photographic slides in cynomolgus monkeys (*Macaca fascicularis*). *Primates, 33,* 407-412.

Lauer, E.W. (1945). The nuclear pattern and fibre connections of certain basal telencephalic centers in the macaque. *Journal of Comparative Neurology, 82,* 215-254.

Lazarus, J. (1990). Looking for trouble. *New Scientist,* 62-65.

Leavens, D.A., Hopkins, W.D., & Bard, K.A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 110,* 346-353.

LeDoux, J.E. (1987). Emotion. In: V.B. Mountcastle, F. Plum, & S.R. Geiger (Eds.), *Handbook of physiology section I: The nervous system volume V: higher functions of the brain, part I.* (pp. 419-459). Bethesda, Maryland: American Physiological Society.

LeDoux, J.E. (1991). Emotion and the limbic system concept. *Concepts in Neuroscience, 2,* 169-199.

LeDoux, J.E. (1996). *The emotional brain: The mysterious underpinnings of emotional life.* New York: Simon and Schuster.

Leekam, S., Baron-Cohen, S., Perrett, D.I., Milders, M., & Brown, S. (1997). Eye-direction detection: a dissociation between geometric and joint attention skills in autism. *British Journal of Developmental Psychology, 15,* 77-95.

Leichnetz, G.R., & Astruc, J. (1977). The course of some prefrontal corticofugals to the pallidum, substantia innominata, and amygdaloid complex in monkeys. *Experimental Neurology, 54,* 104-109.

Leichnetz, G.R., & Goldberg, M.E. (1988). Higher centers concerned with eye movement and visual attention: cerebral cortex and thalamus. In: Buttner & Ennever (Eds.), *Neuroanatomy of the oculomotor system.* (pp. 365-429). Amsterdam: Elsevier Science Publishers BV (Biomedical Division).

Leonard, C.M., Rolls, E.T., Wilson, F.A.W., & Baylis, G.C. (1985). Neurons in the amygdala of the monkey with responses selective for faces. *Behavioural Brain Research, 15,* 159-176.

Leslie, A.M. (1987). Pretense and representation: the origins of "theory of mind". *Psychological Review, 94,* 412-426.

Leslie, A.M., & Frith, U. (1988). Autistic children's understanding of seeing, knowing and believing. *British Journal of Developmental Psychology, 6,* 315-324.

Leung, E.H.L., & Rheingold, H.L. (1981). Development of pointing as a social gesture. *Developmental Psychology, 17,* 215-220.

Linnankoski, I, Gronroos, M., & Pertovaara, A. (1993). Eye contact as a trigger of male sexual arousal in stump-tailed macaques (*Macaca arctoides*). *Folia Primatologia, 60,* 181-184.

Lipp, H.P. (1978). Aggression and flight behaviour of the marmoset monkey, Callithrix jacchus: an ethnogram for brain stimulation studies. *Brain, Behavior and Evolution, 15,* 241-259.

Lipp, H.P., & Hunsperger, R.W. (1978). Threat, attack and flight elicited by electrical stimulation of the ventromedial hypothalamus of the marmoset monkey, Callithrix jacchus. *Brain, Behavior and Evolution, 15,* 260-293.

Lloyd, R.L., & Kling, A.S. (1991). Delta activity from amygdala in squirrel monkeys (*Saimiri sciureus*): influence of social and environmental context. *Behavioural Neuroscience, 105,* 223-229.

Lloyd, S.A.C., & Dixson, A.F. (1988). Effects of hypothalamic lesions upon the sexual and social behaviour of the male common marmoset (*Callithrix jacchus*). *Brain Research, 463,* 317-329.

MacLean, P.D. (1952). Some psychiatric implications of physiological studies on frontotemporal portion of limbic system. *Electroencephalography and Clinical Neurophysiology, 4,* 407-418.

MacPhail, E.M. (1982). *Brain and intelligence in vertebrates.* Oxford: Clarendon Press.

MacPhail, E.M. (1996). Cognitive function in mammals: the evolutionary perspective. *Cognitive Brain Research, 3,* 279-290.

Maestripieri, D. (1996). Gestural communication and its cognitive implications in pigtail macaques (*Macaca nemestrina*). *Behaviour, 133,* 997-1022.

Maestripieri, D. (1996). Social communication among captive stump-tailed macaques (*Macaca arctoides*). *International Journal of primatology, 17,* 785-802.

Markowitsch, H.J., Emmans, D., Irle, E., Streicher, M., & Preilowski, B. (1985). Cortical and subcortical afferent connections of the primate's temporal pole:A study of rhesus monkeys, squirrel monkey, and marmosets. *Journal of Comparative Neurology, 242,* 425-458.

Marler, P. (1977) Evolution of communication. In: T.A. Sebeok (Ed.), *How animals communicate..* Bloomington: Indiana University Press.

Marlowe, W.B., Mancall, E.L., & Thomas, J.J. (1975). Complete Kluver-Bucy syndrome in man. *Cortex, 11,* 53-59.

Martin, A., Wiggs, C.L., Ungerleider, L.G., & Haxby, J.V. (1996). Neural correlates of category-specific knowledge. *Nature, 379,* 649-652.

Martin, K.A.C. (1988). The Wellcome prize lecture: From single cells to simple circuits in the cerebral cortex. *Quarterly Journal of Experimental Physiology, 73,* 637-702.

Martin, P., & Bateson, P. (1993). *Measuring behaviour: an introductory guide.* Cambridge, UK: Cambridge University Press.

Martin, R.D. (1996). Scaling of the mammalian brain: the maternal energy hypothesis. *News in Physiological Sciences, 11,* 149-156.

Maunsell, J.H.R. & Newsome, W.T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience, 10,* 363-401.

Mass, & Kling, A. (1975). Social behavior in stump-tailed macaques (*Macaca speciosa*) after lesions of the dorsolateral frontal cortex. *Primates, 16,* 239-252.

Mehler, W. (1980). Subcortical afferent connections of the amygdala in the monkey. *Journal of Comparative Neurology, 190,* 733-762.

Melnick, D.J., & Pearl, M.C. (1987). Cercopithecines in multimale groups: genetic diversity and population. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies.* (pp. 121-134). Chicago: University of Chicago Press.

Meltzoff, A.N., & Moore, M.K. (1977). Imitation of facial and manual gestures by human neonates. *Science, 198,* 75-78.

Mendelson, M.J., Haith, M.M., & Goldman-Rakic, P.S. (1982). Face scanning and responsiveness to social cues in infant rhesus monkeys. *Developmental Psychology, 18,* 222-228.

Menzel, E.W. (1971). Communication about the environment in a group of young chimpanzees. *Folia Primatologia, 15,* 220-232.

Menzel, E.W. (1973). Leadership and communication in young chimpanzees. In: E.W. Menzel (Ed.), *Precultural primate behavior: Symposium IV of the International Congress of Primatology.*

Menzel, E.W. (1974a). Communication and aggression in a group of young chimpanzees. In: P. Pliner, L. Krames, & T. Alloway (Eds.), *Nonverbal communication of aggression.* (pp. 103-133). New York: Plenum Press.

Menzel, E.W. (1974b). A group of young chimpanzees in a one-acre field. In: A.M. Schrier & F. Stollnitz (Eds.), *Behaviour of non-human primates.* (pp. 83-153). New York: Academic Press.

Menzel, E.W. (1979). Communication of object-locations in a group of young chimpanzees. In: D.A. Hamburg & E.R. McCom (Eds.), *The great apes.* (pp. 359-371). Menlo Park, CA: Benjamin Cummings Publishing Co.

Menzel, E.W., & Halpern, S. (1975). Purposive behavior as a basis for objective communication between chimpanzees. *Science, 189,* 652-654.

Merrill, E.G. & Ainsworth, A. (1972). Glass-coated platinum-plated tungsten microelectrodes. *Medical and Biological Engineering,* 10, 662-672.

Mesulam, M.M., & Mufson, E.J. (1982). Insula of the old world monkey I: architectonics in the insula-orbito-temporal component of the paralimbic brain. *Journal of Comparative Neurology, 212,* 1-22.

Mesulam, M.M., & Mufson, E.J. (1982). Insula of the old world monkey III: efferent cortical output and comments on function. *Journal of Comparative Neurology, 212,* 38-52.

Mesulam, M.M., & Mufson, E.J. (1984). Neural inputs into the nucleus basalis of the substantia innominata (Ch4) in the rhesus monkey. *Brain, 107,* 253-274.

Mikami, A., Nakamura, K., & Kubota, K. (1994). Neuronal responses to photographs in the superior temporal sulcus of the rhesus monkey. *Behavioural Brain Research, 60,* 1-13.

Milders, M.V., & Perrett, D.I. (1993). Recent developments in the neuropsychology and physiology of face processing. *Balliere's Clinical Neurology,* 2, 361-388.

Miller, M.H. (1976). Dorsolateral frontal lobe lesions and behavior in the macaque: dissociation of threat and aggression. *Physiology and Behaviour, 17,* 209-213.

Miller, M.H., & Levine, E.R. (1977). Effects of orbitofrontal lesions on social behavior in a confined group of stump-tail macaques (Macaca speciosa). *Primates, 18,* 903-912.

Miller, R.E. (1967). Experimental approaches to the physiological and behavioral concomitants of affective communication in rhesus monkeys. In: S.A. Altmann (Ed.), *Social communication among primates.* (pp. 125-134). Chicago: University of Chicago Press.

Miller, R.E. (1974). Nonverbal expressions of aggression and submission in social groups of primates. In: P. Pliner, L. Krames, & T. Alloway (Eds.), *Nonverbal communication of aggression.* (pp. 135-160). New York: Plenum Press.

Milton, K. (1988). Foraging behavior and the evolution of primate intelligence. In: R.W. Byrne & A. Whiten (Eds.) *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans.* (pp.285-305). Oxford: Oxford University Press.

Mineka, S., Davidson, M., Cook, M., & Keir, R. (1984). Observational conditioning of snake fear in rhesus monkeys. *Journal of Abnormal Psychology, 93,* 355-372.

Mirsky, A.F., Rosvold, H.E., & Pribram, K.H. (1957). Effects of cingulectomy on social behavior in monkeys. *Journal of Neurophysiology, 20,* 588-601.

Mishkin, M. (1978). Memory in monkeys severely impaired by combined but not by separate removal of amygdala and hippocampus. *Nature, 273,* 297-298.

Mishkin, M., & Aggleton, J.P. (1981). Multiple functional contributions of the amygdala in the monkey. In: Y. Ben-Ari (Ed.), *The amygdaloid complex: INSERM symposium no.20.* (pp. 409-420). Amsterdam: Elsevier/North Holland Biomedical Press.

Mishkin, M., Ungerleider, L.G., & Macko. K.A. (1983). Object vision and spatial vision:two cortical pathways. *Trends In Neurosciences, 6,* 414-417.

Mistlin, A.J. (1988). *Neural mechanisms underlying the perception of socially relevent stimuli in the macaque monkey.* Unpublished Doctoral Thesis, University of St Andrews.

Mistlin, A.J., & Perrett, D.I. (1990). Visual and somatosensory processing in the macaque temporal cortex: the role of 'expectation'. *Experimental Brain Research, 82,* 437-450.

Mitchell, P. (1996). *Introduction to theory of mind: Children, autism and apes.* London: Arnold.

Mithen, S. (1996). The early prehistory of human social behaviour: issues of archaeological inference and cognitive evolution. *Proceedings of the British Academy, 88,* 145-177.

Miyashita, Y., Date, A., & Okuno, H. (1993). Configurational encoding of complex visual forms by single neurons of monkey temporal cortex. *Neuropsychologia, 31,* 1119-1131.

Mizuno, N., Uchida, K., Nomura, S., Nakamura, Y., Sugimoto, T., & Uemura-Sumi, M. (1981). Extrageniculate projections to the visual cortex in the macaque monkey: an HRP study. *Brain Research, 212,* 454-459.

Moran, M.A., Mufson, E.J., & Mesulam, M.M. (1987). Neural inputs into the temporopolar cortex of the rhesus monkey. *Journal of Comparative Neurology, 256,* 88-103.

Morecraft, R.J., Geula, C., & Mesulam, M.M. (1992). Cytoarchitecture and neural afferents of orbitofrontal cortex in the brain of the monkey. *Journal of Comparative Neurology, 323,* 341-358.

Morel, A., & Bullier, J. (1990). Anatomical segregation of two cortical visual pathways in the macaque monkey. *Visual Neuroscience, 4,* 555-578.

Morissette, P., Ricard, M., & Decarie, T.G. (1995). Joint visual attention and pointing in infancy: a longitudinal study of comprehension. *British Journal of Developmental Psychology, 13,* 163-175.

Morris, D. (1967). *The naked ape.* London: Triad Grafton Book.

Morris, J.S., Frith, C.D., Perrett, D.I., Rowland, D., Young, A.W., Calder, A.J., & Dolan, R.J. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature, 383,* 812-815.

Mufson, E.J., & Mesulam, M.M. (1982). Insula of the old world monkey II: afferent cortical input and comments on the claustrum. *Journal of Comparative Neurology, 212,* 23-37.

Mufson, E.J., Mesulam, M.M., & Pandya, D.N. (1981). Insular interconnections with the amygdala in the rhesus monkey. *Neuroscience, 6,* 1231-1248.

Mundy, P., Sigman, M., Ungerer, J., & Sherman, T. (1986). Defining the social deficits of autism: the contribution of non-verbal communication measures. *Journal of Child Psychology and Psychiatry, 27,* 657-669.

Murray, E.A., & Gaffan, D. (1994). Removal of the amygdala plus subjacent cortex disrupts the retention of both intramodal and crossmodal associative memories in monkeys. *Behavioural Neuroscience, 108,* 494-500.

Myers, R.E., Swett, C., & Miller, M. (1973). Loss of social group affinity following prefrontal lesions in free-ranging macaques. *Brain Research, 64,* 257-269.

Nahm, F.K.D., Tranel, D., Damasio, H., & Damasio, A.R. (1993). Cross-modal associations and the human amygdala. *Neuropsychologia, 31,* 727-744.

Nakamichi, M., & Yoshida, A. (1986). Discrimination of mother by infant among Japanese macaques (*Macaca fuscata*). *International Journal of Primatology, 7,* 481-489.

Nakamura, K., Matsumoto, K., Mikami, A.A., & Kubota, K. (1994). Visual response properties of single neurons in the temporal pole of behaving monkeys. *Journal of Neurophysiology, 71(3),* 1206-1221.

Nakamura, K., Mikami, A., & Kubota, K. (1992). Activity of single neurons in the monkey amygdala during performance of a visual discrimination task. *Journal of Neurophysiology, 67,* 1447-1463.

Nauta, W.J.H. (1961). Fibre degeneration following lesions of the amygdaloid complex in the monkey. *Journal of Anatomy, 95,* 515-530.

Newsome, W.T., Britten, K.H., Saltzman, C.D., & Movshon, J.A. (1990). Neuronal mechanisms of motion perception. *Cold Spring Harbor Symposia of Quantitative Biology. 55,* 697-705.

Nishida, T. (1987). Local traditions and cultural transmission. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W.Wrangham and T.T. Struhsaker (Eds.) *Primate societies* (pp. 462-474). Chicago: University of Chicago Press.

Nishijo, H., Ono, T., & Nishino, H. (1988a). Topographic distribution of modality-specific amygdalar neurons in alert monkey. *Journal of Neuroscience, 8,* 3556-3569.

Nishijo, H., Ono, T., & Nishino, H. (1988b). Single neuron responses in amygdala of alert monkey during complex sensory stimulation with affective significance. *Journal of Neuroscience, 8,* 3570-3583.

Norita, M., & Kawamura, K. (1980). Subcortical afferents to the monkey amygdala: an HRP study. *Brain Research, 190,* 225-230.

Norusia, M.J. (1993). Cluster analysis. In: M.J. Norusia (Ed.) *SPSS for Windows: Professional statistics. release 6.0.* (pp. 155-222). Chicago: SPSS Inc.

O' Connell, S.M. (1996). *Theory of mind in chimpanzees.* Unpublished Doctoral Thesis, University of Liverpool.

O' Scalaidhe, S., Albright, T.D., Rodman, H.R., & Gross, C.G. (1995). Effects of superior temporal polysensory area lesions on eye movements in the macaque monkey. *Journal of Neurophysiology, 73,* 1-19.

Ono, T., Fukuda, M., Nishino, H., Sasaki, K., & Muramoto, K. (1983). Amygdaloid neuronal responses to complex visual stimuli in an operant feeding situation in the monkey. *Brain Research Bulletin, 11,* 515-518.

Ono, T., Tamura, R., Nishijo, H., Nakamura, K., & Tabuchi, E. (1989). Contribution of amygdalar and lateral hypothalamic neurons to visual information processing of food and nonfood in monkey. *Physiology and Behaviour, 45,* 411-421.

Oram, M. W. (1996) Unpublished neurophysiology and statistical analysis programs written in Turbo PASCAL.

Oram, M.W., & Perrett, D.I. (1992). Time course of neural responses discriminating different views of the face and head. *Journal of Neurophysiology, 68,* 70-83.

Oram, M.W., & Perrett, D.I. (1994). Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli. *Journal of Cognitive Neuroscience, 6,* 99-116.

Oram, M.W., & Perrett, D.I. (1996). Integration of form and motion in the anterior superior temporal polysensory area (STPa) of the macaque monkey. *Journal of Neurophysiology, 76,* 109-129.

Oram, M.W., Perrett, D.I., & Hietanen, J.K. (1993). Directional tuning of motion-sensitive cells in the anterior superior temporal polysensory area of the macaque. *Experimental Brain Research, 97,* 274-294.

Oram, M.O, Perrett, D. I, Wachsmuth, E and Emery, N. J (1997) Coding of limb, body-part and whole body motion in the anterior superior polysensory area (STPa) of the macaque monkey. *Cerebral Cortex,* (in review).

Orbach, J., & Kling, A. (1964). The stump-tailed macaque: A docile Asiatic monkey. *Animal Behaviour, 12,* 343-348.

Packer, C. (1977). Reciprocal altruism in *Papio anubis. Nature, 265,* 441-443.

Packer, C., & Ruttan, L. (1988). The evolution of cooperative hunting. *American Naturalist, 132,* 159-198.

Pandya, D.N., & Rosene, D.L. (1993). Laminar patterns of thalamic, callosal and association afferents in the primary auditory area of the rhesus monkey. *Experimental Neurology, 119,* 220-234.

Pandya, D.N., Van Hoesen, G.W., & Domesick, V.B. (1973). A cingulo-amygdaloid projection in the rhesus monkey. *Brain Research, 61,* 369-373.

Pandya, D.N., Van Hoesen, G.W., & Mesulam, M.M. (1981). Efferent connections of the cingulate gyrus in the rhesus monkey. *Experimental Brain Research, 42,* 319-330.

Pandya, D.N., & Yeterian, E.H. (1985). Architecture and connections of cortical association areas. In: A. Peters & E.G. Jones (Eds.), *Cerebral cortex vol.4.* (pp. 3-61). Oxford, and New York: Plenum Publishing Corporation.

Pandya, D.N., & Yeterian, E.H. (1990). Prefrontal cortex in relation to other cortical areas in rhesus monkey: architecture and connections. *Progress in Brain Research, 85,* 63-93.

Parent, A., Mackey, A., & De Bellefeuille, L. (1983). The subcortical afferents to caudate nucleus and putamen in primate: A fluorescence retrograde double labeling study. *Neuroscience, 10,* 1137-1150.

Passingham, R.E. (1993). *The frontal lobes and voluntary action.* Oxford, UK: Oxford University Press.

Pawlowski, B., Lowen, C.B., & Dunbar, R.I.M. (1997). Neocortex size, social skills and mating success in primates. *Ethology,* (in review).

Perrett, D.I., & Emery, N.J. (1994). Understanding the intentions of others from visual signals: neurophysiological evidence. *Cahiers de Psychologie Cognitive, 13,* 683-694.

Perrett, D.I., Harries, M.H., Benson, P.J., Chitty, A.J., & Mistlin, A.J. (1990a). Retrieval of structure from rigid and biological motion: an analysis of the visual response of neurons in the macaque temporal cortex. In: A. Blake and T. Troscianko (Eds.) *AI and the eye,* (pp. 181-201). Chichester: Wiley.

Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K., & Ortega, J.E. (1989a). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology, 146,* 87-114.

Perrett, D.I., Harries, M.H., Chitty, A.J., & Mistlin, A.J. (1990b). Three stages in the classification of body movements by visual neurons. In: H. B. Barlow, C. Blakemore and M. Weston-Smith (Eds.) *Images and understanding.* (pp. 94-107) Cambridge: Cambridge University Press.

Perrett, D.I., Harries, M.H., Mistlin, A.J., & Chitty, A.J. (1990c). Recognition of objects and actions: frameworks for neuronal computation and perceptual experience. In: D.M. Guthrie (Ed.), *Higher-order sensory processing.* (pp. 155-173). Manchester: Manchester University Press.

Perrett, D.I., Harries, M.H., Mistlin, A.J., Hietanen, J.K., Bevan, R., Thomas, S., Ortega, J.O., Oram, M.W., & Brierly, K. (1990d). Social signals analysed at the single cell level: someone's looking at me, something touched me, something moved! *International Journal of Comparative Psychology, 4,* 25-55.

Perrett, D.I., Hietanen, J.K., Oram, M.W., & Benson, P.J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 335,* 23-30.

Perrett, D.I., May, K.A., & Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. *Nature, 368,* 239-242.

Perrett, D.I., & Mistlin, A.J. (1990). Perception of facial characteristics by monkeys. In: W.C. Stebbins & M.A. Berkley (Eds.), *Comparative Perception.* (pp. 187-215). New York: John Wiley.

Perrett, D.I., Mistlin, A.J., & Chitty, A.J. (1987). Visual cells responsive to faces. *Trends In Neuroscience, 10,* 358-364.

Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A.J., Potter, D.D., Broennimann, R., & Harries, M. (1988). Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. *Behavioural Brain Research, 29,* 245-258.

Perrett, D.I., Mistlin, A.J., Harries, M.H., & Chitty, A.J. (1989b). Understanding the visual appearance and consequence of hand actions. In: M.A. Goodale (Ed.) *Vision and Action: The Control of Grasping.* (pp. 163-180), New Jersey: Ablex Publishing Co.

Perrett, D.I., & Oram, M.W. (1993). Neurophysiology of shape processing. *Image and Vision Computing, 11,* 317-333.

Perrett, D.I., Oram, M.W., Harries, M.H., Bevan, R., Hietanen, J.K., Benson, P.J., & Thomas, S. (1991). Viewer-centred and object-centred coding of heads in the macaque temporal cortex. *Experimental Brain Research, 86,* 159-173.

Perrett, D.I., Oram, M.W., & Wachsmuth, E. (1993). Understanding minds and expression from facial signals: studies at the brain cell level. In: *Proceedings of the Second IEEE International Workshop on Robot and Human Communication Supplement, 3-5 November 1993,* Tokyo, Japan, 3-12.

Perrett, D.I., Rolls, E.T., & Caan, W. (1979). Temporal lobe cells of the monkey with visual responses selective for faces. *Neuroscience Letters, S3,* S358.

Perrett, D.I., Rolls, E.T., & Caan, W. (1982). Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research, 47,* 329-342.

Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S.P., Broennimann, R., Milner, A.D., & Jeeves, M.A. (1985a). Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: A preliminary report. *Behavioural Brain Research, 16,* 153-170.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., & Jeeves, M.A. (1985b). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London: Biological Sciences, 223,* 293-317.

Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S.M., & Jeeves, M.A. (1984). Neurons responsive to faces in the temporal cortex: studies of functional organization, sensitivity to identity and relation to perception. *Human Neurobiology, 3,* 197-208.

Perryman, K.M., Kling, A.S., & Lloyd, R.L. (1987). Differential effects of inferior temporal cortex lesions upon visual and auditory-evoked potentials in the amygdala of the squirrel monkey (*Saimiri sciureus*). *Behavioural and Neural Biology, 47,* 73-79.

Peters, M., & Ploog, D. (1976). Frontal lobe lesions and social behavior in the squirrel monkey (Saimiri): A pilot study. *Acta Biol Med Germ, 35,* 1317-1326.

Phelps, M.T., & Roberts, W.A. (1994). Memory for pictures of upright and inverted primate faces in humans (Homo sapiens), Squirrel monkeys (*Saimiri sciureus*), and pigeons (*Columba livia*). *Journal of Comparative Psychology, 108,* 114-125.

Pitkanen, A., & Amaral, D.G. (1991). Demonstrations of projections from the lateral nucleus to the basal nucleus of the amygdala: a PHA-L study in the monkey. *Experimental Brain Research, 83,* 465-470.

Ploog, D. (1981). Neurobiology of primate audio-vocal behavior. *Brain Research Reviews, 3,* 35-61.

Plotnik, R. (1968). Changes in social behavior of squirrel monkeys after anterior temporal lobectomy. *Journal of Comparative and Physiological Psychology, 66,* 369-377.

Porrino, L.J., Crane, A.M., & Goldman-Rakic, P.S. (1981). Direct and indirect pathways from the amygdala to the frontal lobe in rhesus monkeys. *Journal of Comparative Neurology, 198,* 121-136.

Povinelli, D.J. (1987). Monkeys, apes, mirrors and minds: the evolution of self-awareness in primates. *Human Evolution, 2,* 493-509.

Povinelli, D.J. (1996). Chimpanzee theory of mind? the long road to strong inference. In: P. Carruthers & P.K. Smith (Eds.), *Theories of theories of mind.* (pp. 293-329). Cambridge: Cambridge University Press.

Povinelli, D.J., Bierschwale, D.T., Reaux, J.E., & Cech, C.G. (1997). Do juvenile chimpanzees understand attention as a mental state? *Journal of Comparative Psychology,* (in press).

Povinelli, D.J., & Davis, D.R. (1994). Differences between chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*) in the resting state of the index finger: implications for pointing. *Journal of Comparative Psychology, 108,* 134-139.

Povinelli, D.J., & Eddy, T.J. (1994). The eyes as a window: what young chimpanzees see on the other side. *Cahiers de Psychologie Cognitive, 13,* 695-705.

Povinelli, D.J., & Eddy, T.J. (1996a). Factors influencing young chimpanzees' (*Pan troglodytes*) recognition of 'attention'. *Journal of Comparative Psychology, 110,* 336-345.

Povinelli, D.J., & Eddy, T.J. (1996b). Chimpanzees: joint visual attention. *Psychological Science, 7,* 129-135.

Povinelli, D.J., & Eddy, T.J. (1996c). What young chimpanzees know about seeing. *Monographs of the Society for Research in Child Development, 61, Serial No. 247.*

Povinelli, D.J., & Eddy, T.J. (1997). Specificity of gaze-following in young chimpanzees. *British Journal of Developmental Psychology,* (in press).

Povinelli, D.J., Nelson, K.E., & Boysen, S.T. (1990). Inferences about guessing and knowing by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 104,* 203-210.

Povinelli, D.J., Nelson, K.E., & Boysen, S.T. (1992). Comprehension of role reversal in chimpanzees: evidence of empathy? *Animal Behaviour, 43,* 633-640.

Povinelli, D.J., Parks, K.A., & Novak, M.A. (1991). Do rhesus monkeys (*Macaca mulatta*) attribute knowledge and ignorance to others? *Journal of Comparative Psychology, 105,* 318-325.

Povinelli, D.J., Parks, K.A., & Novak, M.A. (1992). Role reversal by rhesus monkeys, but no evidence of empathy. *Animal Behaviour, 43,* 269-281.

Povinelli, D.J., Rulf, A., & Bierschwale, D.T. (1994). Absence of knowledge attribution and self-recognition in young chimpanzees (*Pan troglodytes). Journal of Comparative Psychology, 108,* 74-80.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 4,* 515-526.

Preuss, T.M., & Goldman-Rakic, P.S. (1991). Myelo- and cytoarchitecture of the granular frontal cortex and surrounding regions in the strepsirhine primate *Galago* and the anthropoid primate *Macaca. Journal of Comparative Neurology, 310,* 429-474.

Preuss, T.M., & Goldman-Rakic, P.S. (1991). Architectonics of the parietal and temporal association cortex in the strepsirhine primate Galago compared to the anthropoid primate Macaca. *Journal of Comparative Neurology, 310,* 475-506.

Price, J.L. (1981). The efferent projections of the amygdaloid complex in the rat, cat and monkey. In: Ben-Ari-Y (Ed.), *The amygdaloid complex: Inserm symposium no. 20.* (pp. 121-132). Amsterdam: Elsevier/North Holland.

Price, J.L. (1981). Toward a consistent terminology for the amygdaloid complex. In: Y. Ben-Ari (Ed.), *The amygdaloid complex: Inserm symposium no. 20.* (pp. 13-18). Amsterdam: Elsevier/North Holland.

Price, J.L., & Amaral, D.G. (1981). An autoradiographic study of the projections of the central nucleus of the monkey amygdala. *Journal of Neuroscience, 1(11),* 1242-1259.

Puce, A., Allison, T., Gore, J.C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology, 74,* 1192-1199.

Purvis, A. (1995). A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 348,* 405-421.

Purvis, A., & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): An Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences, 11,* 247-251.

Raleigh, M.J., Brammer, G.L., McGuire, M.T., & Yuwiler, A. (1985). Dominant social status facilitates the behavioral effects of serotonergic agonists. *Brain Research, 348,* 274-282.

Raleigh, M.J., Brammer, G.L., Yuwiler, A., Flannery, J.W., McGuire, M.T., & Geller, E. (1980). Serotonergic influences on the social behavior of vervet monkeys (*Cercopithecus aethiops sabaeus*). *Experimental Neurology, 68,* 322-334.

Raleigh, M.J., McGuire, M.T., Brammer, G.L., Pollack, D.B., & Yuwiler, A. (1991). Serotonergic mechanisms promote dominance acquisition in adult male vervet monkeys. *Brain Research, 559,* 181-190.

Raleigh, M.J., McGuire, M.T., Melega, W., Cherry, S., Huang, S.-C., & Phelps, M. (1996). Neural mechanisms supporting successful social decisions in simians. In: A.R. Damasio, H. Damasio, & Y. Christen (Eds.), *Neurobiology of Decision-Making*. (pp. 63-82). Berlin: Springer Verlag.

Raleigh, M.J., & Steklis, H.D. (1981). Effects of orbitofrontal and temporal neocortical lesions on the affiliative behavior of vervet monkeys (Cercopthecus aethiops sabeus). *Experimental Neurology, 73*, 378-389.

Raleigh, M.J., Steklis, H.D., Ervin, F.R., Kling, A.S., & McGuire, M.T. (1979). The effects of orbitofrontal lesions on the aggressive behavior of vervet monkeys (*Cercopithecus aethiops sabaeus*). *Experimental Neurology, 66*. 158-168.

Rauschecker, J.P., Tian, B., & Hauser, M. (1995). Processing of complex sounds in the macaque nonprimary auditory cortex. *Science, 268*, 111-114.

Redican, W.K. (1975). Facial expressions in nonhuman primates. In: L.A. Rosenblum (Ed.), *Primate behavior: developments in field and laboratory research*. (pp. 104-194). New York: Academic Press.

Ristau, C.A. (1991a). Before mindreading: attention, purposes and deception in birds? In: A. Whiten (Ed.), *Natural theories of mind*. (pp. 209-222). Oxford: Blackwell Publishers.

Ristau, C. A. (1991b, Ed.). *Cognitive ethology: the minds of other animals*. Hillsdale: Lawrence Erlbaum Associates, Publishers.

Rizzolatti, G., Fadiga, L., Gallese, V, & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*, 131-141.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V, Paulesu, E., Perani, D., & Fazio, F. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research, 111*, 246-252.

Rizzolatti, G., Gentilucci, M., Camarda, R.M., Gallese, V, Luppino, G., Matelli, M., & Fogassi, L. (1990). Neurons related to reaching-grasping arm movements in the rostral part of area 6 (area 6ab). *Experimental Brain Research, 82*, 337-350.

Roberts, W.A., & Mazmanian, D.S. (1988). Concept learning at different levels of abstraction by pigeons, monkeys and people. *Journal of Experimental Psychology: Animal Behavior Processes, 14*, 247-260.

Robinson, B.W. (1967). Vocalization evoked from forebrain in *Macaca mulatta*. *Physiology and Behaviour, 2*, 345-354.

Rodman, H.R., Scalaidhe, P.O., & Gross, C.G. (1993). Response properties of neurons in temporal cortical visual areas of infant monkeys. *Journal of Neurophysiology, 70*. 1115-1136.

Rolls, E.T. (1981). Responses of amygdaloid neurons in the primate. In: Y. Ben-Ari (Ed.) *The amygdaloid complex: Inserm symposium no. 20*. (pp. 383-394). Amsterdam: Elsevier/North Holland.

Rolls, E.T. (1984). Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. *Human Neurobiology, 3*, 209-222.

Rolls, E.T. (1991). Neurophysiology and functions of the primate amygdala. In: J.P. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction*. (pp. 143-166). New York: Wiley-Liss.

Rolls, E.T., Burton, M.J., & Mora, F. (1976) Hypothalamic neuronal responses associated with the sight of food. *Brain Research, 111,* 53-66.

Rosene, D.L., & Van Hoesen, G.W. (1977). Hippocampal efferents reach widespread areas of cerebral cortex and amygdala in the rhesus monkey. *Science, 198,* 315-317.

Rosenfeld, S.A., & Van Hoesen, G.W. (1979). Face recognition in the rhesus monkey. *Neuropsychologia, 17,* 503-509.

Rosvold, H.E., Mirsky, A.F., & Pribram, K.H. (1954). Influence of amygdalectomy on social behaviour in monkeys. *Journal of Comparative and Physiological Psychology, 47,* 173-178.

Rumelhart, D.E., & McClelland, J.L. (1986, Eds.). *Parallel distributed processing.* Cambridge, MA: MIT Press

Russchen, F.T., Amaral, D.G., & Price, J.L. (1985). The afferent connections of the substantia innominata in the monkey, *Macaca fascicularis. Journal of Comparative Neurology, 242,* 1-27.

Russchen, F.T., Bakst, I, Amaral, D.G., & Price, J.L. (1985). The amygdalostriatal projections in the monkey. An anterograde tracing study. *Brain Research, 329,* 241-257.

Russon, A.E. (1997). The nature and evolution of intelligence in orangutans (*Pongo pygmaeus*). *Primates,* (in press).

Sackett, G.P. (1965). Response of rhesus monkeys to social stimulation presented by means of coloured slides. *Perceptual and Motor Skills, 20,* 1027-1028.

Sackett, G.P. (1966). Monkeys reared in isolation with pictures as visual input: evidence for an innate releasing mechanism. *Science, 154,* 1468-1473.

Sade, D.S. (1973). An ethogram for rhesus monkeys. I: Antithetical contrasts in posture and movement. *American Journal of Physical Anthropology, 38,* 537-542.

Saleem, K.S., & Tanaka, K. (1996). Divergent projections from the anterior inferotemporal area TE to the perirhinal and entorhinal cortices in the macaque monkey. *Journal of Neuroscience, 16,* 4757-4775.

Sambrook, T.D. (1995). *Social complexity in a large and small group of olive baboons.* Unpublished Doctoral Thesis, University of St Andrews.

Sambrook, T.D., & Whiten, A. (1997). On the nature of complexity in cognitive and behavioural science. *Theory and Psychology, 7,* 191-213.

Sands, S.F., Lincoln, C.E., & Wright, A.A. (1982). Pictorial similarity judgements and the organization of visual memory in the rhesus monkey. *Journal of Experimental Psychology: General, 111,* 369-389.

Sanghera, M.K., Rolls, E.T., & Roper-Hall, A. (1978). Visual responses of neurons in the dorsolateral amygdala of the alert monkey. *Experimental Neurology, 63,* 610-626.

Saper, C.B., Swanson, L.W., & Cowan, W.M. (1978). The efferent connections of the anterior hypothalamic area of the rat, cat and monkey. *Journal of Comparative Neurology, 182,* 575-600.

Saper, C.B., Swanson, L.W., & Cowan, W.M. (1979). Some efferent connections of the rostral hypothalamus in the squirrel monkey and cat. *Journal of Comparative Neurology, 184,* 205-242.

Sarter, M., & Markowitsch, H.J. (1985). Involvement of the amygdala in learning and memory: a critical review, with emphasis on anatomical relations. *Behavioural Neuroscience, 99,* 342-380.

Saunders, R.C., & Rosene, D.L. (1988). A comparison of the efferents of the amygdala and the hippocampal formation in the rhesus monkey: I. Convergence in the entorhinal, prorhinal, and perirhinal cortices. *Journal of Comparative Neurology, 271,* 153-184.

Saunders, R.C., Rosene, D.L., & Van Hoesen, G.W. (1988). Comparison of the efferents of the amygdala and the hippocampal formation in the rhesus monkey: II. Reciprocal and non-reciprocal connections. *Journal of Comparative Neurology, 271,* 185-207.

Saver, J.L., & Damasio, A.R. (1991). Preserved access and processing of social knowledge in a patient with acquired sociopathy due to ventromedial frontal damage. *Neuropsychologia, 29,* 1241-1249.

Sawaguchi, T. (1990). Relative brain size, stratification, and social structure in anthropods. *Primates, 31,* 257-272.

Sawaguchi, T. (1992). The size of the neocortex in relation to ecology and social structure in monkeys and apes. *Folia Primatologia, 58,* 131-145.

Sawaguchi, T., & Kudo, H. (1990). Neocortical development and social structure in primates. *Primates, 31,* 283-289.

Scaife, M. (1976). The response to eye-like shapes by birds. II: the importance of staring, pairedness and shape. *Animal Behaviour, 24,* 200-206.

Scaife, M. (1976). The response to eye-like shapes by birds. I: the effect of context: a predator and a strange bird. *Animal Behaviour, 24,* 195-199.

Scaife, M., & Bruner, J.S. (1975). The capacity for joint visual attention in the infant. *Nature, 253,* 265-266.

Scannell, J.W., Sengpiel, F., Tovee, M.J., Benson, P.J., Blakemore, C., & Young, M.P. (1996). Visual motion processing in the anterior ectosylvian sulcus of the cat. *Journal of Neurophysiology, 76,* 895-907.

Schaller, G.B. (1964). *The year of the gorilla.* Chicago: University Press.

Schmahmann, J.D., & Pandya, D.N. (1991). Projections to the basis pontis from the superior temporal sulcus and superior temporal region in the rhesus monkey. *Journal of Comparative Neurology, 308,* 224-248.

Schrier, A.M., Angarella, R., & Povar, M.L. (1984). Studies of concept formation by stumptailed monkeys: concepts humans, monkeys and letter A. *Journal of Experimental Psychology: Animal Behavior Processes, 10,* 564-584.

Schrier, A.M., & Brady, P.M. (1987). Categorization of natural stimuli by monkeys (*Macaca mulatta*): effects of stimulus set size and modification of exemplars. *Journal of Experimental Psychology: Animal Behavior Processes, 13,* 136-143.

Schwartzbaum, J.S. (1965). Discrimination behaviour after amygdalectomy in monkeys: visual and somesthetic learning and perceptual capacity. *Journal of Comparative and Physiological Psychology, 60(3),* 314-319.

Schwartzbaum, J.S., & Poulos, D.A. (1965). Discrimination behaviour after amygdalectomy in monkeys: learning set and discrimination reversals. *Journal of Comparative and Physiological Psychology, 60(3),* 320-328.

Schwartzbaum, J.S., Wilson, W.A., & Morrisette, J.R. (1961). The effects of amygdalectomy on locomotor activity in monkeys. *Journal of Comparative and Physiological Psychology, 54,* 334-336.

Scott, S.K., Young, A.W., Calder, A.J., Hellawell, D.J., Aggleton, J.P., & Johnson, M. (1997). Impaired auditory recognition of fear and anger following bilateral amygdala lesions. *Nature, 385,* 254-257.

Scott, T.R., Karadi, Z., Oomura, Y., Nishino, H., Plata-Salaman, C.R., Lenard, L., Giza, B.K., & Aou, S. (1993). Gustatory neural coding in the amygdala of the alert macaque monkey. *Journal of Neurophysiology, 69(6),* 1810-1820.

Seltzer, B., & Pandya, D.N. (1978). Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the Rhesus monkey. *Brain Research, 149,* 1-24.

Seltzer, B., & Pandya, D.N. (1989a). Frontal lobe connections of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology, 281,* 97-113.

Seltzer, B., & Pandya, D.N. (1989b). Intrinsic connections and architectonics of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology, 290,* 451-471.

Seltzer, B., & Pandya, D.N. (1991). Post-Rolandic cortical projections of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology, 312,* 625-640.

Seltzer, B., & Pandya, D.N. (1994). Parietal, temporal and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer. *Journal of Comparative Neurology, 343,* 445-463.

Semendeferi, K., Damasio, H., Frank, R., & Van Hoesen, G.W. (1997). The evolution of the frontal lobes: a volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. *Journal of Human Evolution, 32,* 375-388.

Seyfarth, R.M., and Cheney, D.L. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour, 40,* 754-764.

Seyfarth, R.M., Cheney, D.L., & Marler, P. (1980a). Monkey response to three different alarm calls: Evidence of predator classification and semantic communication. *Science, 210,* 801-803.

Seyfarth, R.M., Cheney, D.L., & Marler, P. (1980b). Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour, 28,* 1070-1094.

Shepard, R.N. (1962). The analysis of proximities: Multidimensional scaling with an unknown distance function. I. *Psychometrika, 27,* 125-140.

Singh, S.D. (1976). Sociometric analysis of the effects of the bilateral lesions of frontal cortex on the social behaviour of rhesus monkeys. *Indian Journal of Psychology, 51*, 144-160.

Smuts, B.B. (1985) *Sex and friendship in baboons.* Hawthorne, NY: Aldine.

Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., & Struhsaker, T.T. (1987, Eds.). *Primate societies.* Chicago: University of Chicago Press.

Snedecor, G.W., & Cochran, W.G. (1980). *Statistical methods.* Ames, Iowa: Iowa State University Press.

Stephan, H., Frahm, H., & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologia, 35*, 1-29.

Stephan, H., Frahm, H.D., & Baron, G. (1987). Comparison of brain structure volumes in insectivora and primates VII: amygdaloid components. *Journal of Hirnforsch, 5*, 571-584.

Stephan, H., & Pirlot, P. (1970). Volumetric comparisons of brain structures in bats. *Zeitschrift fur Zodogisches Systematik und Evolutions-forschung, 8*, 200-236.

Suomi, S.J., Harlow, H.F., & Lewis, J.K. (1970). Effect of bilateral frontal lobectomy on social preferences of rhesus monkeys. *Journal of Comparative and Physiological Psychology, 70*, 448-453.

Swartz, K.B. (1983). Species discrimination in infant pigtail macaques with pictorial stimuli. *Developmental Psychobiology, 16*, 219-231.

Tanaka, K. (1993). Neuronal mechanisms of object recognition. *Science, 262*, 685-688.

Tanaka, K., Saito, H., Fukada, Y., & Moriya, M. (1991). Coding visual images of objects in the inferotemporal cortex of the macaque monkey. *Journal of Neurophysiology, 66*, 170-189.

Tanji, J. & Shima, K. (1994). Role for supplementary motor area cells in planning several movements ahead. *Nature, 371*, 413-416.

Thompson, C.I. (1981). Long-term behavioural development of rhesus monkeys after amygdalectomy in infancy. In: Y. Ben-Ari (Ed.), *The Amygdaloid Complex: Inserm symposium 20.* (pp. 259-270). Amsterdam: Elsevier/North Holland.

Thompson, C.I., Bergland, R.M., & Towfighi, J.T. (1977). Social and nonsocial behaviours of adult rhesus monkeys after amygdalectomy in infancy or adulthood. *Journal of Comparative and Physiological Psychology, 91(3)*, 533-548.

Thompson, C.I., Schwartzbaum, J.S., & Harlow, H.F. (1969). Development of social fear after amygdalectomy in infant rhesus monkeys. *Physiology and Behaviour, 4*, 249-254.

Thompson, C.I., & Towfighi, J.T. (1976). Social behavior of juvenile rhesus monkeys after amygdalectomy. *Physiology and Behaviour, 17*, 831-836.

Thomsen, C.E. (1974). Eye contact by non-human primates toward a human observer. *Animal Behaviour, 22*, 144-149.

Thorpe, S.J., Rolls, E.T., & Maddison, S. (1983). The orbitofrontal cortex: neuronal activity in the behaving monkey. *Experimental Brain Research, 49,* 93-115.

Thrumble, K. (1987) *An examination into the acquisition and temporal modification of tool use stratergies by captive stumptail macaques.* Unpublished Bsc (Hons) Thesis, University of St Andrews.

Thrumble, K., & Perrett, D.I. (1987). The acquisition of tool use behaviour in a social colony of stumptail macaques. *Association for the Study of Animal Behaviour*, (abstract).

Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: S.T. Parker & K.R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: comparative developmental approaches.* (pp. 274-311). Cambridge: Cambridge University Press.

Tomasello, M. (1996). Do apes ape? In: C.M. Heyes & B.G. Galef (Eds.), *Social learning in animals: the roots of culture.* (pp. 319-346). San Diego: Academic Press Inc.

Tomasello, M., & Call, J. (1997). *Primate cognition.* New York: Oxford University Press (in press).

Tomasello, M., Call, J., & Hare, B. (1997). Five primate species follow the visual gaze of conspecifics. (in review, unpublished manuscript)

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of tool-use by young chimpanzees. *Human Evolution, 2,* 175-183.

Tomasello, M., Kruger, A.C., & Ratner, H.H. (1993) Cultural learning. *Behavioural and Brain Sciences, 16,* 495-552.

Tomonaga, M. (1994). How laboratory-raised japanese monkeys (*Macaca fuscata*) perceive rotated photographs of monkeys: Evidence for an inversion effect in face perception. *Primates, 35,* 155-165.

Tomonaga, M., Itakura, S., & Matsuzawa, T. (1993). Superiority of conspecific faces and reduced inversion effect in face perception by a chimpanzee. *Folia Primatologia, 61,* 110-114.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In: J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted Mind: Evolutionary psychology and the generation of culture.* (pp. 19-136). New York: Oxford University Press.

Tranel, D., & Damasio, A.R. (1993). The covert learning of affective valence does not require structures in hippcampal sstem or amygdala. *Journal of Cognitive Neuroscience, 5,* 79-88.

Turner, B.H. (1981). The cortical sequence and terminal distribution of sensory related afferents to the amygdaloid complex of the rat and monkey. In: Y. Ben-Ari (Ed.), *The amygdaloid complex: Inserm symposium no. 20.* (pp. 51-62). Amsterdam: Elsevier/North Holland.

Turner, B.H., Gupta, K.C., & Mishkin, M. (1978). The locus and cytoarchitecture of the projection areas of the olfactory bulb in Macaca mulatta. *Journal of Comparative Neurology, 177,* 381-396.

Turner, B.H., Mishkin, M., & Knapp, M. (1980). Organization of the amygdalopetal projections from modality-specific cortical association areas in the monkey. *Journal of Comparative Neurology, 191*. 515-543.

Ungerleider, L.G., & Desimone, R. (1986). Projections to the superior temporal sulcus from the central and peripheral field representations of V1 and V2. *Journal of Comparative Neurology, 248*. 147-163.

Ungerleider, L.G., & Mishkin, M. (1982). Two cortical visual systems. In: D. J. Ingle, M. A. Goodale and R. J. W. Mansfield (Eds.) *Analysis of visual behaviour*. (pp. 549-586). Cambridge, MA: MIT Press.

Valentine, T., & Bruce, V. (1986). The effect of race, inversion and encoding activity upon face recognition. *Acta Psychologia, 61*, 259-273.

Van Hoesen, G.W. (1981). The differential distribution, diversity and sprouting of cortical projections to the amygdala in the rhesus monkey. In: Y. Ben-Ari (Ed.), *The amygdaloid complex: Inserm symposium no. 20*. (pp. 77-90). Amsterdam: Elsevier/North Holland.

Van Hoesen, G.W., & Pandya, D.N. (1975). Some connections of the entorhinal (area 28) and perirhinal (area 35) cortices of the rhesus monkey.I.Temporal lobe afferents. *Brain Research, 95*. 1-24.

van Hoof, J.A.R.A.M. (1962). Facial expressions in higher primates. *Symposium of the Zoological Society of London, 8*, 97-125.

van Hoof, J.A.R.A.M. (1967). The facial displays of the catarrhine monkeys and apes. In: D. Morris (Ed.), *Primate ethology*. (pp. 7-68). London: Weidenfeld and Nicholson.

van Lawick-Goodall, J. (1971) *In the shadow of man*. London: Collins.

van Schaik, C.P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*, 120-144.

van Schaik, C.P., & van Hooff, J.A.R.A.M. (1983). On the ultimate causes of primate social systems. *Behaviour, 85*, 91-117.

van Schaik, C.P., van Noordwijk, M.A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in Sumatran forest primates. *Primates, 24*, 211-221.

Visalberghi, E., & Fragaszy, D.M. (1990). Do monkeys ape? In: S.T. Parker & K.R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes: comparative developmental approaches*. (pp. 247-273). Cambridge: Cambridge University Press.

von Bonin, G., & Bailey, P. (1947). *The neocortex of macaca mulatta*. Urbana, Illinois: University of Illinois Press.

Wachsmuth, E (1995). *Coding of object parts, view, orientation and size in the temporal cortex of the macaque*. Unpublished Doctoral Thesis, University of St Andrews.

Wachsmuth, E., Oram, M.W., & Perrett, D.I. (1994). Recognition of objects and their component parts: responses of single units in the temporal cortex of the macaque. *Cerebral Cortex, 5*. 509-522.

Wada, J.A. (1961). Modification of cortically induced responses in brain stem of shift of attention in monkeys. *Science, 133*, 40-42.

Waddell, P.J., & Penny, D. (1996). Evolutionary trees of apes and humans from DNA sequences. In: A. Lock and C.R. Peters (Eds.) *Handbook of symbolic evolution*. (pp. 53-73). Oxford: Clarendon Press.

Walker, A.E., Thomson, A.F., & McQueen. J.D. (1953). Behavior and the temporal rhiencephalon in the monkey. *John Hopkins Bulletin, 93,* 65-93.

Walters, J.R. (1987). Kin recognition in non-human primates. In: D.J.C. Fletcher & C.D. Michener (Eds.), *Kin recognition in animals.* (pp. 359-393). New York: John Wiley & Sons, Ltd.

Walters, J.R., & Seyfarth, R.M. (1987). Conflict and co-operation. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate societies.* (pp. 306-317). Chicago: University of Chicago Press.

Weiskrantz. (1956). Behavioral changes associated with ablations of the amygdaloid complex in monkeys. *Journal of Comparative and Physiological Psychology, 49,* 381-391.

Whiten, A. (1994). Grades of mindreading. In: C. Lewis & P. Mitchell (Eds.), *Origins of an understanding of mind.* (pp. 47-70). Hillsdale, NJ: Lawrence Erlbaum Associates.

Whiten, A. (1996a). When does smart behaviour-reading become mind-reading? In: P. Carruthers & P.K. Smith (Eds.), *Theories of theories of mind.* (pp. 277-292). Cambridge: Cambridge University Press.

Whiten, A. (1996b). Imitation, pretence and mindreading: secondary representation in comparative primatology and developmental psychology? In: A.E. Russon, S.T. Parker, & K.A. Bard (Eds.), *Reaching into thought.* (pp. 300-324). Cambridge: Cambridge University Press.

Whiten, A. (1997a). The Machiavellian mindreader. In: A. Whiten & R.W. Byrne (Eds.), *Machiavellian intelligence II: Evaluations and extensions.* Cambridge: Cambridge University Press, (in press).

Whiten, A. (1997b). Evolutionary and developmental origins of the mindreading system. In: J. Langer & M. Killen (Eds.), *Piaget, evolution and development.* London: Lawrence Erlbaum, (in press).

Whiten, A., & Byrne, R.W. (1988a). The manipulation of attention in primate tactical deception. In: R.W. Byrne & A. Whiten (Eds.), *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans.* (pp. 211-223). Oxford: Oxford University Press.

Whiten, A., & Byrne, R.W. (1988b). Tactical deception in primates. *Behavioral and Brain Sciences, 11,* 233-273.

Whiten, A., & Byrne, R.W. (1997, Eds.). *Machiavellian intelligence II: Evaluations and extensions.* Cambridge: Cambridge University Press, (in press).

Whiten, A., Custance, D.M., Gomez, J.C., Texidor, P. & Bard, K.A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 110,* 3-14.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In: P.J.B. Slater, J.S. Rosenblatt, C. Beer, & M. Milinski (Eds.), *Advances in the study of behavior.* (pp. 239-283). New York: Academic Press, Inc.

Whitlock, D.G., & Nauta, W.J.H. (1956). Subcortical projections from the temporal neocortex in macaca mulatta. *Journal of Comparative Neurology, 106,* 183-212.

Wilson, F.A.W., O' Scalidhe, P., & Goldman-Rakic, P.S. (1993). Dissociation of object and spatial processing domains in the primate prefrontal cortex. *Science, 260,* 1955-1958.

Wilson, F.A.W., & Rolls, E.T. (1993). The effects of stimulus novelty and familiarity on neuronal activity in the amygdala of monkeys performing recognition memory tasks. *Experimental Brain Research, 93,* 367-382.

Wimmer, H. & Perner, J. (1983). Beliefs about beliefs: representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition, 13,* 103-128.

Wrangham, R.W. (1987). Evolution of social structure. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & Struhsaker, T.T. (Eds.) *Primate societies.* (pp. 282-296). Chicago: University of Chicago Press.

Wright, A.A., & Roberts, W.A. (1996). Monkey and human face perception: inversion effects for human, but not monkey faces or scenes. *Journal of Cognitive Neuroscience, 8,* 278-290.

Wu, H.M.H., Holmes, W.G., Medina, S.R., & Sackett, G.P. (1980). Kin preference in infant *Macaca nemestrina. Nature, 285,* 225-227.

Yamane, S., Kaji, S., & Kawano, K. (1988). What facial features activate face neurons in the inferotemporal cortex of the monkey? *Experimental Brain Research, 73,* 209-214.

Yeterian, E.H., & Pandya, D.N. (1989). Thalamic connections of the cortex of the superior temporal sulcus in the rhesus monkey. *Journal of Comparative Neurology, 282,* 80-97.

Yeterian, E.H., & Pandya, D.N. (1991). Corticothalamic connections of the superior temporal sulcus in rhesus monkeys. *Experimental Brain Research, 83,* 268-284.

Yin, R.K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology, 81,* 141-145.

Yoshikubo, S. (1985). Species discrimination and concept formation by rhesus monkeys (*Macaca mulatta*). *Primates, 26,* 285-299.

Young, F.W. (1970). Nonmetric multidimensional scaling: recovery of metric information. *Psychometrika, 35,* 455-473.

Young, F.W. and Harris, D.F. (1993). Multidimensional scaling. In: M.J. Norusis (Ed.), *SPSS for Windows: Professional statistics. release 6.0.* (pp. 155-222). Chicago: SPSS Inc.

Young, A.W., Aggleton, J.P., Hellawell, D.J., Johnson, M., Broks, P., & Hanley, J.R. (1995). Face processing impairments after amygdalectomy. *Brain, 118,* 15-24.

Young, A.W., Hellawell, D.J., Van de Wal, C., & Johnson, M. (1996). Facial expression processing after amygdalotomy. *Neuropsychologia, 34,* 31-39.

Young, M.P. (1992). Objective analysis of the topological organization of the primate cortical visual system. *Nature, 358,* 152-155.

Young, M.P. (1993). The organization of neural systems in the primate cerebral cortex. *Proceedings of the Royal Society of London: Biological Sciences, 252,* 13-18.

Young, M.P. and Scannell, J.W. (1993). Analysis and modelling of the organisation of the mammalian cerebral cortex. In: H.G. Othmer et al (Eds.). *Experimental and theoretical advances in biological pattern formation.* (pp 369-384). New York: Plenum Press.

Young, M.P., Scannell, J.W., O Neil, M.A., Hilgetag, C.C., Burns, G., & Blakemore, C. (1995). Non-metric multidimensional scaling in the analysis of neuroanatomical connection data and the organization of the primate cortical visual system. *Philosophical Transactions of the Royal Society of London: Biological Sciences, 348,* 281-308.

Young, M.P., & Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science, 256,* 1327-1331.

Young, M.P., & Yamane, S. (1993). An analysis at the population level of the processing of faces in the inferotemporal cortex. In: T. Ono, L.R. Squire, M.E. Raichle, D.I. Perrett and M. Fukuda (Eds.) *Brain Mechanisms of Perception and Memory: From Neuron to Behaviour.* (pp. 47-70). New York: Oxford University Press.

Yukie, M., Takeuchi, H., Hasegawa, Y., and Iwai, E. (1990). Differential connectivity of inferotemporal area TE with the amygdala and the hippocampus in the monkey. In: E., Iwai & M. Mishkin (Eds.) *Vision, memory and the temporal lobe* (pp. 129-135). New York:Elsevier Science Publishing Co.,Inc.

Zayan, R. (1994). Mental representation in the recognition of conspecific individuals. *Behavioural Processes, 33,* 233-246.

Zeller, A.C. (1987). Communication by sight and smell. In: B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Struhsaker (Eds.), *Primate Societies.* (pp. 433-439). Chicago: University of Chicago Press.

Zeller, A.C. (1992). Communication in the social unit. In: F.D. Burton (Ed.), *Social processes and mental abilities in non-human primates: Evidence from longitudinal field studies.* (pp. 61-89). Lewiston, NY: Edwin Mellen Press.

Zola-Morgan, S., Squire, L.R., Alvarez-Royo, P., & Clower, R.P. (1991). Independence of memory functions and emotional behavior: separate contributions of the hippocampal formation and the amygdala. *Hippocampus. 1,* 207-220.

Appendix One: Anatomical database of amygdalo-cortical and amygdalo-amygdala connections in the macaque brain. This table displays the general connections of each individual amygdala nucleus (efferent, afferetn and reciprocal connections) and the references the connections were reported in.

Amygdala Nuclei	Connected Areas (Cortical/Amygdala)	References
Lateral Nucleus	Efferent: MT, V4t, A35, Hipp, KA, A12, A6, A25, LB, MB, CTA, PAC, Co, Me, AAA, AHA Afferent: A7a, A23, A9, A10, A14, PaI, TS2, Tpt, TH, TF Reciprocal: PITv, PITd, CITv, CITd, AITv, AITd, STPp, STPa, ER, TGv, TGd, Ig, Id, A13, AB, Ce	B & DeO 90, I & Y 87, S & R 88a, A & P 84, M & Muf 82, I, A & C 87, M et al 85, M, Muf & M 87, A 85, Muf, M & P 81, N 61, S & W 93, I et al 87, F et al 86, A, P & A 83, H & Van H 76, Muf & M 82, L & A 77, T, M & K 80, A, B & P 80, M et al 81, A et al 92
Lateral Basal Nucleus	Efferent: Hipp, A35, ER, TH, TF, TGd, TS1, G, A45, A6, A25, A25, A7b, A7a, LIP, VIP, MSTd, MSTl, MT, V1, V2, V4, V3, Co, CTA, PAC Afferent: L, PaI Reciprocal: PITd, PITv, CITd, CITv, AITd, AITv, STPp, STPa, TGv, Ig, Id, A14, A12, A9, A10, A46, A32, A24, AAA, MB, AB, Me, Ce	B & DeO 90, I & Y 87, S & R ab, A & P 84, I, A & C 87, P et al 81, J & T 75, A 85, Muf, M & P 81, T et al 82, T, W & T 83, N 61, B, D & U 93, S & W 93, I et al 87, F et al 86, A, P & A 83, M et al 81, H & Van H 76, P, Van H & D 73, P, Van H & M 81, W & N 56, L & A 77, T, M & K 80, A, B & P 80, L & G 88, Van H 81, L 45, A et al 92
Medial Basal Nucleus	Efferent: TGd, G, A14, A13, A12, A45, A6, A23, A24, A25, A32, A7b, A7a, LIP, VIP, LB, CTA, Co, Me, AB, Ce	B & DeO 90, I & Y 87, S & R 88ab, A & P 84, M, M & Mes 87, P et al 81, A 85, Muf, M & P 81, N 61, B, D & V 93, S & W 93, I et al 87, F et

	Afferent: L Reciprocal: AITd, AITv, A35, Hipp, ER, TGv, Ig, Id, A9, A10, A46, AHA, PAC	al 86, H & Van H 76, Muf & M 82, I, A & C 87, L & A 77, T, M & K 80, R & Van H 77, A et al 92
Accessory Basal Nucleus	Efferent: A35, TS3, TGd, paAr, paAc, paAl, KA, TS1, G, RI, A13, A12, A11, A46, A23, A24, A25, A32, A1, A2, A3a, A3b, S2, A7b, A7a, LIP, VIP, MB, Co Afferent: A9, Me, PAC Reciprocal: CITd, CITv, AITd, AITv, Hipp, ER, TGv, PaI, Ig, Id, A14, A10, Ce, AHA, LB, L	B & DeO 90, I & Y 87, S & R 88ab, A & P 84, I, A & C 87, M et al 85, M, Muf & M 87, P et al 81, A 85, Muf, M & P 81, N 61, S & W 93, I et al 87, H & Van H 76, L & A 77, T, M & K 80, A, B & P 80, M et al 81, A et al 92
Central Nulceus	Efferent: TGd, AHA, CTA Afferent: AITd, AITv, STPp, STPa, TS2, PaI, A10, A9, Me Reciprocal: A35, ER, Hipp, TGv, Ig, Id, L, LB, AB, MB, PAC	M & Muf 82, M et al 85, M, Muf & M 87, A 85, F et al 86, I, A & C 87, W & N 56, L & A 77, T, M & K 80, A, B & P 80, H & Van H 76, Muf, M & P 81, A et al 92
Cortical Nulceus	Efferent: CITd, CITv, A35, TS1, Ig, A13, A12, A23, A25, A32 Afferent: TGd, Ce, L, LB, AB, MB Reciprocal: Hipp, ER, TGv, Id, Me, PAC	B & DeO 90, I & Y 87, S & R 88ab, M & Muf 82, M, Muf & M 87, Muf, M & P 81, N 61, F et al 86, I, A & C 87, T. M & K 80, A, B & P 80, A et al 92
Medial Nulceus	Efferent: ER, Ig, AHA, AB, CTA, PAC, Co Afferent: STPp, STPa, Id, A11, A13,	I & Y 87, S & R 88a, M, Muf & M 87, A 85, Muf, M & P 81, F et al 86, A, B & P 80, A et al 92

	A10, A9, A46, A23, A25, L, MB Reciprocal: Hipp, TGv, TGd, Ce, LB	
Periamygdaloid Complex	Efferent: CITd, AITd, AITv, Ig, Id, TS1, PaI, RI, G, A1, A2, A3a, A3b, S2 Afferent: Hipp, L, LB, Co Reciprocal: ER, TGv, TGd, Me, Ce, AB, MB	I & Y 87, A & P 84, I, A & C 87, I et al 87, A 85, A et al 92
Anterior Amygdaloid Area	Efferent: A32, TGv, TGd, Ce, L Afferent: Ig, ER Reciprocal: Id	B & DeO 90, M, Muf & M 87, Muf, M & P 81, I, A & C 87, T, M & K 80, A et al 92
Amygdalo-Hippocampal Area	Efferent: none Afferent: Ce, Me, L Reciprocal: LB, MB, AB	Muf, M & P 81, A 85, A et al 92
Cortical Transition Area	Efferent: TGv, TGd Afferent: L, LB, MB, Ce, Me Reciprocal: Hipp	S & R 88b, M, Muf & M 87, A 85, A et al 92, A 86