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Social Learning and the Influence of Social Context: Studies with Common Marmosets and Olive Baboons

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TR E 340

“I learned the way a monkey learns – by watching its parents”

(Charles, Prince of Wales, quoted in Longford, 1983)

“As capuchins do not imitate, we have no strong grounds at present for expecting that any other species of monkey will be able to do so. In fact, despite the many efforts to find imitative learning in other monkey species, the recent data supporting it are few and ... open to alternative interpretations”

(Visalberghi & Fragaszy, 2002)

Abstract

The traditional layman's view of "monkey see, monkey do" contrasts strikingly with the general opinion of the scientific community, which has all but written off the imitative abilities of monkeys. This thesis presents an argument that proposes various ways in which the existing experimental literature may have led to an underestimation of the social learning abilities of monkeys. Firstly, a literature review of comparative approaches to the study of imitation reveals that species have rarely been tested in truly comparative ways, i.e. by comparing performance on analogous task designs. Furthermore, even when analogous tasks are used, confounds (many of them peculiar to social learning research) may be rife. The first experimental chapter examines the performance of common marmoset subjects on a task designed to be similar to one used to test for imitation in several other primate species. Using this paradigm, clear effects of observation of a skilled demonstrator are found. Moving on to the issue of potential confounds in social learning research, the next three experimental chapters address the issue of the effect of social context on social learning. The first of these studies demonstrates that marmosets' skill learning can be strongly facilitated by close social interaction with a trained demonstrator, a result which contrasts quite strongly with many similar studies involving species with less tolerant social structures. The final four studies therefore involve comparisons between common marmosets (which are very tolerant within their family group) and olive baboons (which have a steeply hierarchical social organisation). It is shown that in the baboons, but not the marmosets, a skilled individual's demonstration quality is impaired by the presence of a dominant observer. Furthermore, the baboons, again in contrast with the marmosets, are inhibited from approaching and jointly interacting with a dominant demonstrator, reducing opportunities for skill transmission.

Declarations

I, Christine Anna Caldwell, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Date...11/4/03.....Signature of Candidate.

I was admitted as a research student in September 1997 and as a candidate for the degree of PhD in September 1997; the higher study for which this is a record was carried out in the University of St Andrews between 1997 and 2002.

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

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Chapter One

DO MONKEYS APE?

“Popular opinion has generally attributed to monkeys the ability to learn by imitation. As will appear later, experimental evidence on the matter has been of a conflicting nature, but in the main it has not supported the popular belief.” So begins the article *Imitation in monkeys* written by Haggerty (1909, p337). Nearly a century on, these words ring so true they might have been written yesterday. This thesis will examine some of the reasons why the experimental literature has provided such fragile evidence for social learning and imitation in monkeys.

Social learning here will be taken to refer to any situation in which the presence, or behaviour, or the products of the behaviour, of one individual influences the learning of another. Such learning has been of interest within the scientific community for many years (for reviews see: Box & Gibson, 1999; Galef, 1998; Heyes & Galef, 1996; Heyes & Ray, 2000; Miklosi, 1999; Nicol, 1995; Russon, 1997; Webster & Fiorito, 2001; Whiten & Ham, 1992; Zentall, 2001; Zentall & Galef, 1988), and there are a number of reasons why the phenomenon of social learning has proven such a popular topic of study. The first of these is that understanding these processes in animals may give us some insight into the evolution of human social learning (and hence, human culture). Secondly, researchers have also addressed the question of the mechanisms underlying various cases of social learning. As defined above, the term social learning implies nothing about the underlying mechanisms, which remain to be identified. However, many authors have differentiated several

possible forms of social learning, in terms of the mechanisms potentially involved, (e.g. Galef, 1988; Heyes, 1994; Whiten & Ham, 1992; Zentall, 2001). Thus, social learning can provide an insight into a species' cognitive abilities. Some of these proposed mechanisms, and the distinctions between them, will be discussed in greater detail in Chapter Two.

Understanding social learning is also of crucial practical importance. Social learning has been proposed to be highly relevant to captive animal welfare, as abnormal behaviours may be socially transmitted. There is now some evidence of this in captive chimpanzees and rhesus monkeys (Hook et al., 2002; Nash, Fritz, Alford, & Brent, 1999). Several authors have also suggested that social learning research may be applicable to reintroduction programs aiming to return captive-born animals to their natural habitat (Beck, 1997; Box, 1991; Brown & Laland, 2001; Custance, Whiten, & Fredman, 2002). Previous reintroduction studies have found that captive-born individuals seem to lack some of the skills crucial to survival in the wild, and pre-release training is now considered to be an essential step in the process. For species that have been shown to learn socially, it seems likely that this could potentially form a significant part of this training.

This thesis will focus specifically on social learning in monkeys (that is, all primates except apes and non-anthropoid primates, such as lemurs), traditionally viewed as the mimics of the animal kingdom, liable to copy actions for the very pleasure of doing so. For some time, this belief also persisted within the academic community, with high-level social learning abilities being attributed to monkeys. The classic example of monkey social learning is that of the Japanese macaques of the

Islet of Koshima. This troop were regularly fed sweet potatoes by the researchers who studied them, and it was observed that one member of the troop had taken to washing sand off the potatoes by rinsing them in sea water. Within a few months, the close associates of this monkey (her mother and playmates) were doing the same, and within a few years, nearly half the troop employed the washing technique. This example was initially reported as a case of animal imitation (e.g. Kawamura, 1959). However, subsequent critiques of this interpretation proposed simpler and more plausible mechanisms to account for the data. Galef (1990) noted that the rate of spread of the behaviour was very slow, much slower than one would expect if imitation had been involved. Furthermore, the number of individuals that washed their food appeared to have increased at a steady pace, not an accelerating one, which one might expect if any kind of social learning was implicated (Lefebvre, 1995a).

As researchers began to define subcategories of social learning, according to the proposed underlying mechanism, further criticisms were levelled at the “imitation” interpretation of this field report. Imitation, defined as “learning to do an act by seeing it done” (Thorndike, 1898, p50; Whiten & Ham, 1992), is clearly much more narrowly specified than social learning generally, and is widely regarded as the most cognitively complex form of social learning (e.g. Byrne, 1995; Galef, 1988; Heyes, 1993).

Of the other social learning mechanisms discerned, the one most relevant here is “stimulus enhancement” (e.g. Galef, 1988; Spence, 1937; Whiten & Ham, 1992). Stimulus enhancement is said to have occurred when the presence of an individual draws an observer’s attention to a particular object or part of an object, thus

enhancing the observer's opportunity to learn about the object. Such a process could easily support the transmission of the potato-washing behaviour, without the need for imitative learning.

Experimental research is required in order that social learning mechanisms can be determined, and imitation can be distinguished from other, simpler, processes of social learning. However, following such experimental investigations, the weight of academic opinion appeared to shift completely. Book chapters with titles such as, *Do monkeys ape?* (Visalberghi & Fragaszy, 1990), and *Social learning in monkeys: primate "primacy" reconsidered* (Fragaszy & Visalberghi, 1996) have contributed to a notion of monkeys as particularly poor social learners, surpassed not only by great apes, but also by birds and perhaps rodents. In a review of the literature on social learning in birds, Lefebvre & Bouchard (in press) point out that for every bird species that has been tested for imitation, positive results have been found. They note that this pattern contrasts particularly strongly with the monkey social learning literature. Similarly, Heyes & Ray (2000), reviewing all the non-human imitation literature, conclude that, "The most promising evidence of imitation in animals presently comes from studies of birds" (p235). And Fragaszy & Visalberghi (1996), reviewing several years' worth of experimental data on social learning in monkeys, state that, "through this work we came to the inescapable conclusion that capuchin monkeys do not acquire instrumental behaviours (such as using a tool, solving a mechanical puzzle, or washing sandy foods) by watching a skilled demonstrator." (p68).

This thesis will aim to address the question of whether the recent reputation of monkeys as poor social learners is justified. Are monkeys truly less gifted in terms of

their social learning abilities in comparison with other groups of animals, or is it possible that the particular studies on which these judgements have been based were not conducive to the detection of social learning and imitation in monkeys?

The issues discussed from here on will primarily concern the social learning of instrumental skills. However, it should be noted that social learning has been found to operate in a number of other spheres, including vocal learning (e.g. Janik & Slater, 2000), mate choice (e.g. Galef & White, 2000), food preferences (e.g. Galef & Wigmore, 1983) and predator recognition (e.g. Mineka & Cook, 1988). The reason these issues will not be considered further is that for each of these types of social learning, there is some evidence that specialised mechanisms may have evolved for this particular purpose. Such mechanisms may therefore be relatively inflexible, and impossible to transfer to novel learning contexts. As such, they probably tell us little about a species' social learning abilities generally, and therefore may contribute little to the clarification of the issues under examination in this thesis.

Thesis Plan

The thesis begins by focusing on mechanistic issues in social learning. The literature review chapter therefore deals with issues involved in making species comparisons of cognitive ability, particularly within social learning research. This review will address the question of whether or not valid species comparisons can realistically be made, and will weigh up the contrasting strengths and weaknesses of alternative methods of doing this. It should be noted that Chapter Two was written subsequent to the completion of much of the experimental work in this thesis, and

therefore some of the data from the later empirical chapters are referred to in this review.

Chapter Three investigates social learning mechanisms in common marmosets. An “artificial fruit” task (a methodology which will be discussed in greater detail in the next two chapters) was used in an attempt to show imitative social learning in these monkeys. The intention of this piece of empirical work was to make use of a methodology analogous to one previously used to test for imitation in several other species of primate, in an attempt to make a valid judgement of relative species ability. The results of this particular study were nonetheless fairly ambiguous with regard to the marmosets’ relative performance compared with other primates, as it proved particularly difficult to replicate the methodology precisely given the limitations of the marmosets’ manipulative competence.

The later empirical chapters (Four, Five and Six) therefore go on to address a slightly different issue, that being the question of how social context effects may be influential in dictating the outcome of social learning experiments, potentially giving rise to misleading differences in species performance.

Chapter Four is a study of the effectiveness of an interactive demonstration (demonstrator and observer together) as compared with a purely observational (demonstrator and observer separated) one, again with common marmoset subjects. The results of this experiment showed a striking effect, with the interactive demonstration strongly facilitating learning compared with the purely observational demonstration.

Having found this result, that joint interaction facilitated social learning, the rest of the thesis addresses the question of whether such learning conditions are available to other species with different social structure. Common marmosets live in closely related family groups, known for the high level of cooperative behaviour (including food sharing) exhibited within that group. In Chapters Five and Six therefore, the aim was to investigate whether there were any apparent social constraints on the transmission of information within a species which lived in an altogether differently structured society. Olive baboons were studied, which generally live in much larger and more loosely related social groups (as compared with the marmosets).

In Chapter Five, opportunities for joint interaction were investigated in terms of variability in the demonstrator's behaviour. It was found that trained baboon demonstrators' performance of a food-finding behaviour were impaired in the presence of more dominant demonstrators, thus reducing possibilities for social learning between such a dyad. Marmosets under similar conditions however (although again tested within their family group) showed no such effect.

In Chapter Six, joint interaction was investigated in terms of the tendency for the observer to approach the demonstrator. It was found that in the baboons individuals were more inhibited from approaching a novel food dish in the presence of a dominant demonstrator, again reducing the possibilities for joint interaction and therefore social learning. The marmosets however were uninhibited by the presence of their alpha female and joint interaction was again common.

It was concluded from these studies, that there may be greater constraints on social transmission within baboon social organisation than within the marmoset family groups. This may be due to the relative genetic relatedness of the groups tested. Although as the group composition of both species was comparable to wild group structures, the patterns found can still be extrapolated to make predictions about diffusion patterns in natural groups.

This and other methodological issues will be discussed in Chapter Seven of the thesis, the general discussion. In this chapter there will also be a further literature review, tying in the empirical work with previous research on social effects on social learning. The literature on social learning in monkeys will also be reviewed, in the light of the data and arguments presented in this thesis. The practical and theoretical relevance of the empirical material will also be considered.

Chapter Two

EVOLUTIONARY PERSPECTIVES ON IMITATION: IS A COMPARATIVE PSYCHOLOGY OF SOCIAL LEARNING POSSIBLE?

This material in this chapter is adapted from Caldwell & Whiten (in press-a).

“Do monkeys ape?”, asked Visalberghi & Frigaszy (1990), to which Byrne & Tomasello (1995) added “Do rats ape?”, followed by Tomasello (1996) asking, “Do apes ape?”. Implicit in these questions is the assumption that some kind of comparison is indeed possible; that there is a singular and definite, albeit as yet undetermined, yes or no answer. However, the contrasting kinds of arguments presented by these different authors would suggest that the field of comparative social learning still lacks any universally accepted solutions. Since studies of social learning across different species have become increasingly common in recent years (e.g. Box & Gibson, 1999; Galef, 1988; Heyes & Galef, 1996; Heyes & Ray, 2000; Miklosi, 1999; Nicol, 1995; Russon, 1997; Tomasello, Savage-Rumbaugh, & Kruger, 1993; Webster & Fiorito, 2001; Whiten, Custance, Gomez, Texidor, & Bard, 1996; Whiten & Ham, 1992; Zentall, 2001), this review aims to outline both the potential theoretical value and the likely pitfalls that are entailed in a comparative approach.

Before beginning to review the area of comparative approaches to social learning, we should ask why researchers are, or perhaps might be, interested in taking such an approach. The body of literature on social learning in animals is now vast and

still growing rapidly, and interest in the topic comes from a wide variety of theoretical perspectives. For instance some researchers have been interested in issues of welfare (e.g. Cloutier, Newberry, Honda, & Alldredge, 2002; Munksgaard, DePassille, Rushen, Herskin, & Kristensen, 2001), or issues of rehabilitation (e.g. Beck, 1997; Box, 1991; Custance et al., 2002), and of course these are questions which are not only of scientific interest, but also extremely important from a practical point of view. However, this review will be concerned only with research that is explicitly comparative, rather than merely “comparative” in the sense that the subjects are non-human which is the case in many of these applied studies, as well as others.

As noted in the previous chapter, the term social learning itself implies nothing about the underlying mechanisms involved, and many authors have therefore defined numerous subcategories of social learning, based on the mechanisms proposed to be involved. However, this review is concerned in particular with the cognitive processes underlying social learning (and methodological issues associated with investigating these), and it is imitation in particular which has been generally regarded as the most cognitively complex form of social learning. Therefore, it will be imitation specifically, “learning to do an act by seeing it done” (Thorndike, 1898, p50; Whiten & Ham, 1992), that forms the main focus of this review from now on.

It should be noted at the outset that this review is by no means intended to represent an exhaustive catalogue of research on social learning (or even imitation) in animals. Rather, the examples given have been selected for their particular pertinence to the points to be made as part of the examination of methodological approaches to the comparative study of social learning. However, although it may appear that certain

species or phyla may have been overlooked, it is hoped that in fact the issues raised will prove relevant across the board in social learning research.

Theoretical Perspectives

So far in the literature, three main theoretical motives for comparing the relative social learning skills of different species can be discerned. The first of these shall henceforth be labelled the *phylogenetic perspective*, which involves the evolutionary tracing of a collection of socio-cognitive abilities, believed to be related. The second will be called the *animal model perspective*, which is principally concerned with identifying a suitable animal model for the study of imitation as a general phenomenon. And finally there is the *adaptational perspective*, whose main aim is to investigate the functional significance of social learning, such as the question of whether there is a relationship between social learning and living in social groups.

THE PHYLOGENETIC PERSPECTIVE

Under this perspective, cognition is studied from a phylogenetic viewpoint, the basic premise being that similar cognitive abilities found in closely related species were likely inherited by each from a common ancestor whose mental capacities can thereby be reconstructed. Research therefore encompasses the identification of both ancestral commonalities and evolutionary differentiation. This approach is set out with great clarity by Byrne (1995), who concludes that, “With the aid of the

comparative method, the evolutionary history of a trait - even a behaviour that leaves no trace to fossilise - can be inferred from its pattern of occurrence in surviving animals.” (p6).

Researchers taking this perspective are typically interested in a whole suite of socio-cognitive skills, including theory of mind, self-awareness and pretense, and may view imitation as a part of this combination of skills (e.g. Parker, 1996; Suddendorf & Whiten, 2001; Tomasello & Call, 1994; Whiten & Byrne, 1991). From this perspective, therefore, the most interesting aspects of social learning are the underlying cognitive abilities. This approach has therefore generally disregarded issues of function or social context, and focussed almost exclusively on analysing cognitive mechanisms in the individual social learner.

It seems to be universally accepted that human beings are the most imitatively prolific species (e.g. Meltzoff, 1988; Meltzoff, 1996), and the phylogenetic approach has generally been characterised by an expectation that the other great apes will be most likely to share imitative abilities with humans, with other taxa following in accordance with their closeness of relationship with *Homo sapiens*. Whilst this view is not always made explicitly apparent, the viewpoint may be manifested either in terms of research focus (selection of great ape subjects for the investigation of animal imitation (e.g. Nagell, Olguin, & Tomasello, 1993; Tomasello et al., 1993; Whiten et al., 1996; Whiten, 1998), or by a judgment (despite the relative scarcity of imitation research on many primate species) that human beings and great apes show advanced forms of imitation, not shared by monkeys (e.g. Byrne, 1995; Parker, 1996; Russon,

Mitchell, Lefebvre, & Abravanel, 1998; Whiten & Byrne, 1991; Whiten & Ham, 1992).

THE ANIMAL MODEL PERSPECTIVE

Like the phylogenetic perspective, the animal model perspective is also concerned primarily with cognitive processes, and the two approaches thus share a common goal of identifying imitative ability in non-humans. In contrast to the phylogenetic perspective's interest in patterns of evolutionary change, the animal model perspective strives to identify similarities. The approach is motivated by the hypothesis that imitation may be a special case of associative learning, hence potentially available to many species.

Heyes (1994) places imitation within the framework of animal learning theory, as a case of response-reinforcer learning, where, "it is the demonstrator, not the learner, who makes the response that is learned" (p225). Heyes & Ray (2000) take this idea further, proposing a new theory of imitation, the Associative Sequence Learning theory. The ASL model suggests that, "development of the imitation mechanism is highly experience-dependent" (Heyes, 2001, p258). Therefore we should not necessarily expect imitative ability to have any phylogenetic specificity. And any individual, regardless of species, would be unable to imitate had the appropriate prior experience been unavailable to them.

Purely experiential theories of imitation are by no means radical, earlier incarnations having been proposed by Holt (1931) and Miller & Dollard (1941) amongst others. Another was recently proposed by Laland & Bateson (2001) who use a connectionist model under which imitative processes are generated purely on the basis of the experience of synchronous behaviours. As Laland and Bateson (2001) point out, what sets these models apart from the models typically proposed by those working from the phylogenetic perspective (e.g. Tomasello & Call, 1997) is that they require no “‘black box’ that is assumed to pre-exist, and to be capable of complex cognition” (p197).

From this perspective, therefore, there are two main reasons why researchers have been interested in comparative data on imitation. Firstly, under the assumption that imitation is an experience-dependent process common to many animals, models of imitation could be tested using a single, well-chosen species. This animal model could then allow an understanding of imitation generally, in all animals, including humans. This rationale is made most explicit by Heyes & Ray (2000), who state, “...the principal significance of imitation in animals lies in its potential to provide insight into the psychological mechanisms of imitation learning.” (p242). Heyes & Ray (2000) therefore go on to review the data on imitation in animals for the purpose of determining which species would provide the most appropriate model, based on prior demonstration of their imitative ability and practical considerations regarding their suitability as a lab animal. In addition to this motivation, however, the models proposed by Heyes (2001) and Laland & Bateson (2001) also give rise to certain predictions about which animals would be likely to be proficient imitators: those that typically perform behaviours in synchrony, such as gregarious bird species, are

proposed in both articles to be the likeliest candidates. Accordingly, both Heyes (2001) and Laland & Bateson (2001) have discussed data on imitation in several different species in terms of the predictions made by their models.

THE ADAPTATIONAL PERSPECTIVE

The adaptational perspective is concerned with resolving the issue of whether social learning is a specialised adaptation associated with social living, or if it is purely an aspect of more general learning processes. Thus far, the majority of recent research stemming from this perspective has been produced by Lefebvre and colleagues (e.g. Lefebvre & Giraldeau, 1996; Lefebvre, Palameta, & Hatch, 1996; Reader & Lefebvre, 2001). However, interest in the possibility of social learning as an adaptive specialisation dates back over 40 years when it was first suggested by Klopfer (1959; 1961). More recently, adaptive specialisation explanations of a wide variety of cognitive and learning processes have become increasingly popular (e.g. Sherry & Schacter, 1987; Shettleworth, 1993; Shettleworth, 1998), and these have been followed by a corresponding resurgence of interest in this approach to social learning (e.g. Lefebvre et al., 1996; Lefebvre, Templeton, Brown, & Koelle, 1997; Templeton, Kamil, & Balda, 1999). The basic prediction of an adaptive specialisation view of learning and cognition is that interspecific variation in learning and/or cognitive ability should correspond to species diversity in terms of ecology. This view of social learning therefore predicts that, as Klopfer (1959) originally suggested, the most proficient social learners will be those species that live in social groups and those that forage opportunistically.

This perspective is therefore concerned primarily with the function of social learning, as opposed to the mechanism, which is the focus of interest of the previous two perspectives. It follows, then, that a further difference between this approach and the others is that this one tends to emphasise social learning generally, rather than just the mechanism of imitation. However, several researchers have made the more specific suggestion that imitation may itself represent an adaptive specialisation (e.g. Lefebvre et al., 1997; Parker, 1996; Russon et al., 1998). Like social learning generally, it is suggested that this skill will be more likely to be found in highly social species (those that live in groups, or those that engage in scramble competition when feeding). More specifically, however, it will only be those species that use complex, difficult-to-learn food searching and handling techniques that possess imitative skill, as opposed to just general social learning abilities. Since the present review is principally concerned with the issue of making meaningful comparisons of social learning mechanism, the arguments presented will be most relevant to this more specific issue of imitation, in relation to the adaptational perspective, rather than social learning generally.

OVERVIEW

Three different perspectives on the comparative study of social learning have been contrasted. This will not be a perfectly neat division and some workers may feel they cannot be so clearly pigeon-holed, or do not subscribe to the “typical” characteristics described here, but it is hoped that this typology will prove useful in

recognising the diversity of perspectives that exist and need to be reconciled if an integrated comparative psychology of social learning is to be achieved.

Each of the models is firmly grounded in evolutionary theory, although they emphasise to differing extents the forces of continuity of descent versus specialisation of adaptation. The animal model perspective, viewing imitation as an ability based on relatively general learning processes, obviously emphasises continuity of descent. The adaptational perspective however, entertains the possibility that imitation and/or social learning are highly specialised adaptations. The phylogenetic perspective views imitation as a specialised adaptation only in the sense that it comes as part of a compound skill package which has proven particularly valuable in a subgroup of the primate order. In this regard, this perspective also acknowledges continuity of descent, as it is assumed that closely related species are likely to share imitative ability. The phylogenetic and adaptational perspective are therefore perhaps best contrasted in terms of Timberlake's (1993) classification of methods of comparing behaviour, the adaptational approach being primarily concerned with evolutionary convergence, and the phylogenetic approach focussing on homologies.

It is not the intent of this review to weigh up the relative merits of the differing perspectives, but rather to consider what kinds of comparative research may be needed to assess their merits, and perhaps better investigate this in future. The issue of which of these perspectives brings us closest to the truth is still open to question, and more importantly, open to empirical question. It seems clear that the different perspectives are currently, to varying extents, somewhat incompatible with one another. For instance, writers within the phylogenetic perspective often seem to

expect that imitation will be found in humans, and then, with ever-decreasing likelihood, in other great apes, old world monkeys, other monkeys, other primates, and so on (see Parker & Gibson (1979) for a review that suggests imitation, amongst other cognitive skills, might show this pattern of distribution). Clearly this is incompatible with the “animal model” view that we can pick any appropriate species and investigate imitation as a general phenomenon. According to the adaptational perspective, again we might not necessarily expect a primate bias, and yet, it would certainly not predict that imitation would be a general phenomenon. Each of the theories therefore generates slightly different predictions about which species would be likely to imitate. However, as yet, the comparative approach to imitation has not provided data which would allow us to reliably assess the relative merits of the different viewpoints.

One reason why research to date does not allow us to draw such conclusions is that work from each viewpoint has tended to reflect underlying assumptions, rather than explicitly testing them. In work from the phylogenetic perspective, discussion does occur over the phylogenetic appearance of imitation (Parker & Gibson, 1979) but it is treated as a given that the data can be used to infer where, phylogenetically, imitation must have appeared as a skill. The animal model perspective has used comparative data in order to address the question of whether imitation could be a product of general learning processes (Heyes, 2001; Laland & Bateson, 2001), but the idea that a suitable animal model can be found (Heyes & Ray, 2000) suggests that a positive answer has already been assumed. It seems that, just as work from the phylogenetic perspective has a tendency to assume that certain species are *incapable* of imitation, the opposite is true of the animal model perspective, whose researchers

are prepared to assume that imitative ability is shared by many species (albeit that existing data may be considered an inadequate demonstration of such; e.g. Heyes 1993). Neither of these perspectives have as yet been used to generate novel predictions about how different species might perform that would differentiate between alternative perspectives. The adaptational perspective appears to have the best track-record in hypothesis-testing, as work from this perspective has set out expressly to test whether social learning is a specialised adaptation. However this is not yet true for complex forms of social learning like imitation, with which this review is principally concerned. Lefebvre et al. (1997) claim to show support for an adaptive specialisation view of imitation. However, as only one species is tested, the data do not allow us to differentiate between alternative explanations. Comparisons of at least two species (for which opposite predictions would be made) are required.

Even when species have been compared with the intention of testing predictions, there may still be ambiguities of interpretation. For instance, researchers investigating adaptational hypotheses in terms of general social learning abilities, have noted that social living biases could arise from experience, rather than specialised genetic disposition. Animals that live in groups obviously have more opportunities to learn that attending to group members can reap rewards, and may show greater tendencies to learn socially as a result. Following this line of reasoning, Templeton et al. (1999) suggest that their results, supporting the adaptational hypothesis in corvid species, could be explained in terms of either adaptive specialisation or “simply the result of ontogeny” (p454). And Carlier & Lefebvre (1996) point out that, “differences in foraging ecology may lead to different learned responses to local reward contingencies as well as natural selection for different genotypes affecting learning. In

some cases, the standard comparative prediction of ecologically-correlated learning differences may therefore not distinguish between adaptive specialisation and general process theories.” (p1197). In fact some work from this perspective has provided support for experiential models of social learning. Dolman, Templeton, & Lefebvre (1996) found that Zenaida doves from a gregarious population learned more effectively from conspecific tutors, whereas individuals taken from a territorial population exhibited a stronger learning effect when the tutor was a heterospecific. The doves were therefore learning from the species that they would have tended to encounter most often in past non-aggressive foraging situations. Dolman et al. (1996) conclude that the results, “suggest that social learning pathways in Zenaida doves are flexible rather than species-specific” (an interpretation that is clearly eminently compatible with the experiential models).

It may emerge that there is more than a grain of truth in the assumptions and expectations associated with each one of the perspectives. Some authors have already presented viewpoints that endeavour to reconcile a phylogenetic and adaptational interpretation of imitation, for example. Russon et al. (1998) view imitation as a specialised adaptation occurring in social species that feed on embedded substrates, but account for the particular imitative facility of great apes in terms of their requiring a highly complex suite of socio-cognitive abilities. “This review leaves an image of imitation as a heterogeneous rather than a homogeneous phenomenon; even mentally, and in only one of the three evolutionary lines that appear to have generated it, it appears to operate via complex sets of mechanisms that incorporate cognitive, motivational, social, and perceptual processes.” (p133). A similar view is expressed by Van Schaik, Deaner, & Merrill (1999), and by Parker (1996), who proposes that

imitation, teaching and mirror self-recognition evolved in the great apes due to the need for extractive foraging based on “intelligent tool use”.

Methodological Approaches

There are several reasons why researchers have been interested in a comparative psychology of social learning, and this has generated numerous publications that treat data on imitation from one of the comparative perspectives mentioned above. There have been two main types of methodological approach to this, these being i) the comparative experiment, in which two or more species are subjected to approximately analogous procedures; and ii) the comparative analysis of results already accumulated in the literature. In the latter, data are evaluated on different species, which have been studied under often quite different conditions. A further, extremely promising comparative approach to social learning, also merits note here. This is the method of systematically reviewing the *total number* of published reports of social learning. This approach is best exemplified by Reader & Laland's (2002) analysis of the relationship between brain size and social learning in primate species. However, this approach is geared towards evaluating a species' *propensity* towards social learning, and can tell us very little about cognitive mechanism. Lefebvre & Bouchard (in press) have used a similar methodology to investigate social learning in birds, and as they point out, much of the data comes from anecdotal reports from amateur observers. It is therefore the first two approaches which will be considered further in this review.

To date, only four research groups have published systematic comparative experiments applying similar tasks to different species. However, many researchers working from different perspectives have carried out comparative literature reviews concerned with the specific issue of imitation and these are considered first.

Accordingly, Table 1 collates details of reviews of imitation in animals, showing the populations which were judged by the authors to have shown evidence of imitation, and also those for which the authors judged the evidence to be either lacking or insufficient. Particular studies that the reviewers cited in support of their conclusions are listed and detailed in the footnotes below. It should be noted that the later reviews have of course been influenced by research that was not published when some of the earlier reviews were written.

Table 2 turns to the experimental literature and displays details of experiments in which more than one species have been tested using the same procedure. However, the table does not cover *all* of those examples in the literature of imitation studies involving more than one species (many of which predate those publications listed, e.g. Haggerty, 1909; and see tables in Tomasello & Call, 1997; and Whiten & Ham, 1992). Those included are the ones which are explicitly testing for species differences, rather than combining the data on more than one species in order to investigate, for example, imitation in non-human primates as a group.

Table 1. - Imitation literature reviews

Species listed are the ones *explicitly stated in the text* of the listed article as having displayed positive evidence of imitative ability (column one), or as having shown a lack of, or providing insufficient evidence of, imitative ability (column two).

Article/chapter	Author's judgement	
	1. Positive evidence of imitation	2. Lack of/insufficient evidence of imitation
Galef (1988)	budgerigars ^{1,2}	pigeons ³
Whiten & Ham (1992)	chimpanzees ^{4,5,6} , dolphins ⁷	monkeys ^{8,9} , orangutans ^{10,11} , gorillas ¹² , rats ¹³ , budgerigars ^{1,2} , pigeons ³
Heyes (1993)	rats ^{13,14} , budgerigars ^{1,2}	
Byrne (1995)	parrots ¹⁵ , orangutans ¹⁶ , chimpanzees ¹⁷ , gorillas ¹⁸ , dolphins ⁷	rats ^{13,14}
Byrne & Tomasello (1995)	apes ^{17,16}	budgerigars ² , rats ^{13,14}
Tomasello & Call (1997)	human children ¹⁹ , human raised apes ^{17,20}	rats ^{13,14}
Shettleworth (1998)	chimpanzees ²¹	rats ^{13,14} , orangutans ²² , pigeons ²³ , quail ²⁴ , parrots ¹⁵
Heyes & Ray (2000)	pigeons ²³ , quail ²⁴	marmosets ²⁵ , chimpanzees ^{21,26,27} , capuchins ²⁸ , rats ^{29,30} , budgerigars ^{1,2} , starlings ³¹ , carib grackles ³²
Zentall (2001)	pigeons ²³ , quail ²⁴ , parrots ¹⁵ , chimpanzees ^{33,17} , dolphins ^{34,35}	capuchins ²⁸ , budgerigars ^{1,2} , rats ^{13,14} , starlings ³¹ , marmosets ²⁵ , ravens ³⁶

¹ Dawson & Foss (1965), ² Galef, Manzig, & Field (1986), ³ Palameta & Lefebvre (1985), ⁴ Hayes & Hayes (1951), ⁵ Hayes & Hayes (1953), ⁶ Gardner & Gardner (1969), ⁷ Taylor & Saayman (1973), ⁸ Hall (1963), ⁹ Ham (1990), ¹⁰ Galdikas (1982), ¹¹ Wright (1972), ¹² Carpenter (1973), ¹³ Heyes & Dawson (1990), ¹⁴ Heyes, Dawson, & Nokes (1992), ¹⁵ Moore (1992), ¹⁶ Russon & Galdikas (1993), ¹⁷ Hayes & Hayes (1952), ¹⁸ Byrne & Byrne (1993), ¹⁹ Meltzoff (1988), ²⁰ Tomasello et al. (1993), ²¹ Whiten et al. (1996), ²² Call & Tomasello (1994), ²³ Zentall, Sutton, & Sherburne (1996), ²⁴ Akins & Zentall (1996), ²⁵ Bugnyar & Huber (1997), ²⁶ Whiten (1998), ²⁷ Myowa (1996), ²⁸ Custance, Whiten, & Fredman (1999), ²⁹ Mitchell, Heyes, Dawson, & Gardner (1998), ³⁰ Gardner (1997), ³¹ Campbell, Heyes, & Goldsmith (1998), ³² Lefebvre et al. (1997), ³³ Custance, Whiten, & Bard (1995), ³⁴ Harley, Xitco, Roitblat, & Herman (1998), ³⁵ Xitco, Harley, & Brill (1998), ³⁶ Fritz & Kotschal (1999b)

Table 2a. - Comparative experimental studies of social learning (Tomasello and colleagues).

Article	Species compared	Task	Demonstration	Results and authors' conclusions
Nagell et al. (1993)	<i>Pan troglodytes</i> , <i>Homo sapiens</i> (2 and 3 years old)	Tool use (raking in out of reach reward)	Adult human demonstration. Each subject sees one of two methods of raking in reward.	All groups were more successful following demonstration. Two year old children reproduced demonstrated method, but chimpanzees did not. <i>Authors' conclusion:</i> Chimpanzees pay attention to task rather than the actions of a demonstrator.
Tomasello et al. (1993)	<i>Pan troglodytes</i> , <i>Pan paniscus</i> (two <i>Pan</i> species combined, rather than compared), <i>Homo sapiens</i> (18 and 30 months old)	Manipulation of 16 novel objects	Adult human demonstration. Each subject sees two actions on each object, and is asked (or has been given prior behavioural training) to "Do what I do".	Children were judged to have matched the demonstrator's actions more closely than the non-human subjects did, apart from apes that had been raised by humans, which performed at the same level as the children. <i>Authors' conclusion:</i> A human-like sociocultural environment is an essential component in the development of human-like imitative learning skills.
Call & Tomasello (1994)	<i>Pongo pygmaeus</i>	Replication of Nagell et al. (1993)		There was no effect of demonstration type on the actions performed by the subjects. <i>Authors' conclusion:</i> Orangutans, like the chimpanzees, were paying attention to the task rather than to the actions of the demonstrator.
Call & Tomasello (1995)	<i>Pongo pygmaeus</i> , <i>Homo sapiens</i> (3 and 4 years old)	Puzzle box containing reward	Adult human demonstration and conspecific demonstration. Each subject sees one of four different actions on the apparatus to obtain a reward.	Human children reproduced the actions of the demonstrator. Orangutans did not, and as a consequence had a very low rate of success. <i>Authors' conclusion:</i> Orangutans are not able to learn an instrumental task through observation

Table 2b. - Comparative experimental studies of social learning (Whiten and colleagues).

Whiten et al. (1996)	<i>Pan troglodytes, Homo sapiens</i> (2, 3 and 4 years old)	“Artificial fruit” (box containing food reward with single locking mechanism)	Adult human demonstration. Each subject sees one of two methods of unlocking apparatus to obtain reward.	Chimpanzees reproduced demonstrator’s method on one component of the task, but achieved demonstrated outcomes through their own techniques more than the children (all age groups). <i>Authors’ conclusion:</i> Results are evidence of imitation in the chimpanzee, although human children imitate with greater fidelity.
Whiten (1998)	<i>Pan troglodytes</i>	“Artificial fruit” (box containing food reward with multiple locks)	Adult human demonstration. Each subject sees one of two methods of unlocking apparatus, and one of two sequential patterns of defense removal	Chimpanzees reproduced both the sequential structure of the actions, and aspects of the techniques that made up the sequence. <i>Author’s conclusion:</i> Results are evidence of imitation of a novel behavioural sequence in the chimpanzee.
Custance et al. (1999)	<i>Cebus apella</i>	Replication of Whiten et al. (1996)		Capuchins reproduced the demonstrator’s method on one component of the task. <i>Authors’ conclusion:</i> Evidence of simple imitation, or possibly “object movement re-enactment” in the capuchin monkey.
Caldwell, Whiten, & Morris (1999)	<i>Callithrix jacchus</i>	Approximate replication of Whiten et al. (1996). See section on Behavioural Propensities	Conspecific demonstration. Each subject saw one of two actions on the apparatus.	Marmosets did not reproduce the complete actions of the trained model. However, groups were compared according to how closely their behaviours matched those of their model, and corresponding differences were found. <i>Authors’ conclusion:</i> Results are suggestive of imitative ability in the marmoset. However, chimpanzees and capuchin monkeys imitate the task with a much greater degree of fidelity.
Stoinski, Wrate, Ure, & Whiten (2001)	<i>Gorilla gorilla gorilla</i>	Replication of Whiten (1998)		Gorillas reproduced the demonstrator’s technique on one component of the task, but did not reproduce the sequential structure of the actions. <i>Authors’ conclusion:</i> Evidence for imitation in gorillas, on a par with that shown by chimpanzees, but, unlike chimpanzees, no evidence of imitation of the behavioural sequence.
Custance, Whiten, Sambrook, & Galdikas (2001)	<i>Pongo pygmaeus</i>	Replication of Whiten (1998)		No significant overall matching tendency, but a correlation between age and degree of matching. <i>Authors’ conclusion:</i> Possible imitative ability in orangutans, limited to those aged 5 and over.

Table 2c. - Comparative experimental studies of social learning (Bering, Bjorklund and colleagues).

Bering, Bjorklund, & Ragan (2000)	<i>Pan troglodytes, Pongo pygmaeus</i>	Deferred imitation of seven actions on objects	Adult human demonstration. Each subject sees one action on each object.	Both species reproduced demonstrated actions, following a 10 minute delay, on approximately half of the trials. <i>Authors' conclusion:</i> Juvenile great apes raised in human-like conditions possess cognitive abilities that allow deferred imitation.
Bjorklund, Bering, & Ragan (2000)	<i>Pan troglodytes, Pongo pygmaeus</i>	Longitudinal study of deferred imitation (data from Bering et al., 2000, compared with performance on failed items and four new items 2 years later)	Adult human demonstration. Each subject sees one action on each object.	Chimpanzee subject showed an improvement in reproduction of demonstrated actions with age. Orangutan subject did not show a significant improvement. <i>Authors' conclusion:</i> Juvenile chimpanzees, like human children, show Piagetian stages of sensorimotor development. Orangutan subjects may have already reached a "mature", although less competent than the chimpanzee, level of performance at initial testing.

Table 2d. - Comparative experimental studies of social learning (Zentall and colleagues)

Zentall et al. (1996)	<i>Columbia livia</i>	Treadle-press task	Conspecific demonstration. Each subject sees a demonstrator that either pecks or steps on the treadle for a food reward.	A correlation was found between the responses seen and those produced by subjects. <i>Authors' conclusion:</i> Evidence of true imitation in pigeons.
Akins & Zentall (1996)	<i>Coturnix japonica</i>	Replication of Zentall et al. (1996)		A correlation was found between the responses seen and those produced by subjects. <i>Authors' conclusion:</i> Evidence of true imitation in quail.

The first research group to publish comparative experiments on imitation was that of Tomasello and colleagues. Their research has focussed on the great apes and children, and has generally concerned the imitation of practical, goal-directed actions involving tool use. Table 2a shows brief details of each of these studies. Our research group at St Andrews (Whiten and colleagues) have also been engaged in comparative experimentation. Table 2b details these publications, the majority of which have involved only one species. However, our group has treated the data comparatively insofar as the same (or at least similar – a point to be returned to in a later section on Behavioural Propensities) testing devices (“artificial fruits”) were used in each, to test for imitation in a variety of primate species, including human children. These devices have also been used by other researchers studying keas, *Nestor notabilis* (Huber, Rechberger, & Taborsky, 2001) and adult human subjects (Horowitz, 2001). Table 2c shows details of studies published by Bjorklund et al. (2000) and Bering et al. (2000). These studies have involved object manipulation, and have compared the developmental stages of imitative ability in chimpanzees and orangutans. Research by Zentall and colleagues on pigeons and quail (Table 2d) has also been included, as both studies (like the artificial fruit experiments) used the same apparatus design, involving treadle-press behaviours for a food reward.

Tables 1 and 2 point to one fairly obvious conclusion, which is that, despite all attempts to forge a coherent comparative psychology of imitation, it is far from being established. Even the briefest inspection of Table 1 shows that authors disagree on the correct interpretation of the data. We are therefore left with the question of how best to proceed in research on social learning in order that we can make comparisons

which are valid and as unambiguous as possible, in order to converge on conclusions that can be generally agreed by the scientific community.

COMPARATIVE LITERATURE REVIEWS

Despite the obvious disagreement between researchers as to which species have and have not been shown to imitate, six out of the nine reviews referred to in Table 1 (Galef, 1988; Heyes, 1993; Heyes & Ray, 2000; Shettleworth, 1998; Whiten & Ham, 1992; Zentall, 2001) all select the same preferred method of testing for imitation (but see Byrne (2002) for a contrary view). Each of these authors refer to the “two-action test” as the most powerful possible control for social learning effects other than imitation. The two-action test was initially employed by Thorndike (Thorndike, 1911/1970, cited in Shettleworth, 1998) who wished to establish whether chicks could imitate a method of escaping from a box. He therefore designed the box such that there were two alternative ways in which this could be done. If observing chicks tended to use the method that they had seen, then it could be concluded that they had imitated. The method was then used by Dawson & Foss (1965), and later identified by Galef (1988) as the standard for tests of imitative ability.

As well as having been used to study imitation in animals, two-action research designs have also been employed to investigate human neonatal imitation (e.g. Meltzoff & Moore, 1977; 1983). This type of design is referred to as the “cross-target method” (Meltzoff, 1996; Whiten, 2002) within developmental psychology. The fact that this methodology appears to have been independently conceived within an

entirely separate field of investigation only serves to further emphasise its power and practicality as a test for imitation.

However, despite some agreement that the two-action method offers the possibility of a gold standard within imitation research, authors are still in disagreement about the interpretation of such research designs. Essentially, the differences of opinion occur because researchers differ in their views of which aspects of social learning are cognitively significant, and therefore merit inclusion within their definition of imitation. The aim of the following sections is to detail which aspects of task designs researchers have considered to be crucial, and illustrate how this has influenced their interpretation of the literature.

Perceptual Opacity

One aspect of response type which has been interpreted as cognitively complex by several authors is the level of *perceptual opacity* (Heyes & Ray, 2000), or the degree to which the perception of oneself performing an action matches that afforded when observing the action demonstrated by another individual. Heyes (1993) gives the example of curtsying. “If I look down when I curtsy, I see something very different from what I see when I look across at somebody else curtsying.” (Heyes, 1993, p1006). Imitating a perceptually opaque action therefore involves translating visual input into motor output, the main feedback being in the form of kinesthetic information (e.g. Mitchell, 1994). Heyes & Ray (2000) suggest that all actions belong somewhere along a continuum of perceptual opacity, with the most opaque actions being those which are actually invisible to the actor, such as head movements and

facial gestures, and the most transparent being distal appendage movements, for which the performer has access to rich visual feedback.

Heyes (2001) identifies this issue as particularly significant in terms of the cognitive demands in imitation: “Many of the psychological requirements for imitation (e.g. detection and analysis of others’ movements, memory, motor control) are also prerequisites for other types of behaviour. The requirement that is unique to imitation, and therefore the distinctive exploratory challenge for theories of imitation, is a mechanism that can translate visual information about the body movements of others into matching motor output.” (p256).

Whiten & Ham (1992) also argue that imitation of perceptually opaque actions is cognitively complex, in that the action must be “re-represented in its original organizational form” (p271) by the imitator. On this basis, they also argued that vocal imitation is less cognitively demanding than movement imitation: “In song learning, the bird does not have to represent what is in effect the model’s representation of the act as it does in the case of visual imitation; instead, it need only adjust its own output until the sound of this matches what it originally heard (one level of representation). This may be an extra dimension in visual imitation that makes it more demanding than vocal imitation in its computational requirements.” (p272). Similarly, Heyes & Ray (2000) include vocalisations as examples of highly transparent actions on their continuum of perceptual opacity, and Zentall (2001) describes vocal imitation as “relatively easy” (p69).

Object Movement Re-enactment

Zentall (2001) takes the perceptual opacity argument slightly further, to argue that copying of highly transparent actions can be accounted for simply in terms of “stimulus matching”, where the observer need only make an association between two sensory stimuli in order to reproduce the behaviour, as exemplified by, “observing someone turning up the volume of a radio - when the knob turns to the right, the volume increases” (p69). This type of process (which can take perceptual transparency to its extreme, involving no need for matching of bodily movements but only the matching of the environmental effect of a behaviour), has been described by Custance et al. (1999) as “object movement re-enactment”. The observer learns about how an object or parts of an object move; and if the object’s movements are associated with a desirable outcome, the observer may be motivated to try to recreate it. On this basis, Heyes (1998; Heyes & Ray, 2000) has suggested that data presented in Whiten et al.’s (1996) chimpanzee artificial fruit experiment does not qualify as imitation, because the observer may be copying only movements of parts of the fruit as it is dismantled. Tomasello (1996) makes a similar criticism, labeling this effect “emulation learning”, rather than object movement re-enactment.

However, some authors have argued that the imitation/object movement re-enactment distinction so implied is a misleading one. Whiten (2000) argues that imitation and certain emulative effects, like object movement re-enactment, should be viewed as a continuum rather than a dichotomy. Whiten & Custance (1996) suggested that, in tool use for example, copying could occur either at the level of limb movement, or at the level of tool movement. The tool could be regarded as an

extension of the limb, and its actions imitated in a similar way. Furthermore, researchers have argued that such social learning about objects may be cognitively complex in its own right (e.g. Byrne & Russon, 1998; Tomasello, 1998; Whiten & Ham, 1992; although in these cases the learning referred to may go beyond what could strictly be defined as object movement re-enactment, involving some understanding of tool function, and/or causality).

Novelty

Another feature that some researchers have identified as being crucial to the nature of imitation is the novelty of the response. Thorndike's original definition of imitation was, "learning to do an act by seeing it done". On this basis, some (e.g. Byrne, 1995; Byrne & Tomasello, 1995) have argued that the imitated response must be a novel one, or it cannot be described as having been *learned* through imitation.

It is important to all researchers to distinguish imitation from social facilitation, in which nothing new is learned. Social facilitation (e.g. Galef, 1988; Thorpe, 1963; Whiten & Ham, 1992; Zajonc, 1965) is generally used to describe a contagious behaviour, in the sense that an individual's response acts as a releaser for the same response on the part of a conspecific. Examples of such responses include yawning in humans, or synchronous nervous flight in birds. However, Byrne (1994) extends the category of social facilitation, labeling it *response facilitation*, in which, "the probability of occurrence of an established behaviour pattern is temporarily increased in the individual's spontaneous repertoire after observation of the same behaviour pattern in a conspecific" (Byrne & Tomasello, 1995, p1417). Thus, response

facilitation would operate, via a priming process (Byrne, 1995; 2002), on *any* response, as opposed to being limited to certain involuntary species-typical behaviours. On this basis Byrne (1995) and Byrne & Tomasello (1995) do not consider Heyes' (Heyes & Dawson, 1990; Heyes et al., 1992) bi-directional control experiment with rats to be evidence of imitation, as the responses required were not novel. Byrne & Tomasello (1995) also reject Galef et al.'s (1986) budgerigar data for the same reason.

However, other researchers have argued that novelty may be a more problematic criterion than researchers such as Byrne and Tomasello have acknowledged (or, for that matter, demonstrated). It is very difficult to assess the full behavioural history of an individual in order to be sure that an action is truly novel, and even then, this may not satisfy some. Byrne (2002) criticises evidence of human neonatal imitation (Meltzoff & Moore, 1977; 1983) as the actions involved are only novel in the, "trivial sense that the infant has never performed them, but there is no doubt that the facial movements are in the child's latent repertoire" (p85).

Whiten & Cusance (1996) have argued that novelty cannot be reduced to an all or none matter, since an individual will probably have, at one time or another, produced all of the muscular movements of which it is physically capable. This makes novelty an issue of recombination of actions, or employing actions in novel contexts, where there will always be some degree of similarity to what the imitator has done before. Zentall (2001) agrees that an existing response directed at a novel object satisfies the novelty criterion, and furthermore has advocated the use of an additional criterion: the baseline (no demonstration) probability of the behaviour must be very

low. This is consistent with one of the most-frequently quoted definitions of imitation, Thorpe's (1963) "reproduction of a novel *or otherwise improbable* act" (p122). Indeed, it appears that this latter criterion is now widely accepted within the field of social learning. A similar recommendation is made by Miklosi (1999). Furthermore, refereed articles have been published entitled "true imitation", based on the reproduction of responses which, although part of the existing repertoire, have been shown to be infrequent during control tests (Voelkl & Huber, 2000; Zentall et al., 1996). Laland & Bateson (2001) have argued against the use of novelty as a criterion altogether, on the basis that, if imitation exists as a phenomenon, it should be "perfectly possible to imitate an entirely familiar action in an entirely unfamiliar context" (p210).

Sequential Structure

Several researchers consider the imitation of a sequence of actions to be cognitively significant, although each has a different reason for proposing this to be the case. Whiten (1998) suggests that imitation of a sequence of actions can be one way to satisfy the novelty criterion, as long as the sequence itself is novel, and the order of the elements is not constrained in any particular way such that the chosen sequence is in fact the most likely approach: "if the subcomponent acts...can be said to be 'in the repertoire', the performance of them so as to match the sequence observed cannot be said to be in the repertoire any more than [a] randomly assigned alternative sequence" (p271-272).

Investigation into imitation of a sequence of actions will also be crucial to testing the Associative Sequence Learning theory of imitation proposed by Heyes & Ray (2000). The ASL theory suggests that individuals develop, through experience, an, “‘imitation repertoire’ - a set of action units that can be imitated when observed in novel sequences” (p240). Clearly, an ability to imitate sequences of actions must be demonstrated in order to test this theory. If no such ability can be identified, the theory would be challenged.

Byrne & Russon (1998) have argued that there are in fact two kinds of imitation which are cognitively very different from one another. The first they label *action level imitation*, in which, “a novel action is added - as an unmodified whole - to an individual’s motor repertoire” (p677). The second, they call *program level imitation*, which involves the representation of the overall structure of an action sequence, including its ultimate and subsidiary goals, a process which they describe as, “a high-level, constructive mechanism”. On this basis, Byrne (1995) has criticised much of the existing imitation literature for using tasks that are not sufficiently complex, and therefore just tapping into action level imitation, overlooking program level imitation.

As yet, the only empirical demonstration of the ability to imitate an arbitrary sequence, utilising the two-action method, has been Whiten's (1998) experiment with chimpanzees (although see also Whiten, Horner, & Marshall-Pescini, in press). The subjects in Whiten’s study were shown one of two different methods of accessing a food reward, the component elements having been ordered differently in each. The chimpanzees tended to produce sequences of actions more like the ones they had seen demonstrated.

Demonstrator Reinforcement

Miklosi (1999) has pointed out that whether or not a demonstrator receives reinforcement for a response may have implications for the cognitive processes involved in reproduction of that action. In Miklosi's view, associative learning models of imitation (such as those proposed by Heyes (1994) and Heyes & Ray (2000) and described in the section regarding the animal model perspective) would be challenged by an ability to imitate unrewarded actions. Indeed, Campbell et al. (1998) acknowledge that the issue of demonstrator reinforcement may be a potentially important one in terms of the cognitive processes underlying imitation. They suggest that their subjects (European starlings) may have learned either about a response, or about a response-food relationship, and suggest that, "[t]o distinguish between these two mechanisms it would be necessary to perform an experiment in which the relationship between the demonstrators' responses and food reward was varied" (p157). Using such a method, Palameta & Lefebvre (1985) found that pigeons only performed a demonstrated behaviour if the tutor bird had been rewarded, and more recently, Akins & Zentall (1998) found that observation of demonstrator reinforcement was vital for quail to reproduce a response.

Whiten & Ham (1992) also point out that, amongst the many anecdotal reports of imitation in animals, those that involve no apparent reward beyond "imitation for imitation's sake" (p264) are typically the most convincing. These examples do not suffer from the criticism that the same behaviour could simply be acquired via a combination of stimulus enhancement and trial-and-error learning. The investigation of imitation of unrewarded actions need not depend entirely on anecdotal reports

however. Custance et al. (1995) found that chimpanzees would imitate novel arbitrary unrewarded actions, if previously provided with food reinforcement for having matched demonstrated behaviours. Therefore the motivation for imitation can be provided within the experimental paradigm, without requiring that the action itself be intrinsically rewarding.

Goal Representation

It could also be argued that in fact rational imitation might be quite dependent on identifying the purpose of a behaviour rather than blindly imitating, and according to some authors, the ability to infer and represent another individual's goal or intention should be a defining component of imitation. Tomasello & Call (1997) draw a distinction between what they label *mimicking* and imitation. Mimicking, "requires that the learner perceive and understand...the bodily movements that another individual has performed", whereas imitation entails that, "the learner must also understand something of the 'intentional' relations ... (i.e. how the behaviour is designed to bring about the goal)" (p310). Using this criterion of imitation, Tomasello & Call (1997) conclude that there is no evidence for imitation in animals, with the possible exception of some great apes that have been raised in a human environment (see Tables 1 and 2a).

Experimentally distinguishing between the processes of imitation and mimicking, as defined by Tomasello and Call, however, is intrinsically extremely difficult. Simply arriving at the same goal certainly does not prove that the imitator

understands the demonstrator's intention. A good copy of another individual's behaviour (whether mimicked or imitated) will tend to bring about the same goal.

Myowa & Matsuzawa (2000) attempted to examine imitation of intention using a variation on the two-action method in which the demonstrator was unsuccessful using one method, and then successful using a different one. Chimpanzees tended to use the method they had seen in the success phase. However, if the subjects perceived "success" (the opening of the manipulated object) as more reinforcing, then this example may simply represent an effect similar to that described by Akins & Zentall (1998), cited in the previous section.

It therefore remains unclear how to investigate this aspect of imitation under controlled experimental conditions. The distinction between mimicking and true imitation has resulted in what may be a distracting over-emphasis on goal-directed behaviours in the imitation literature. As noted in the previous section, reproduction of unrewarded responses may depend on processes distinct from those involved in reward-related copying, and therefore both merit investigation in their own right.

Deferred Imitation

The ability to imitate actions some time after the original demonstration has also been viewed as a cognitively significant achievement. Deferred imitation has long been considered to be important in developmental psychology. The Piagetian (e.g. Piaget, 1962) stage model asserts that deferred imitation requires "symbolic" representation, i.e. the representation of actions in long-term memory stores. Meltzoff (e.g. Meltzoff, 1988; 1995) has expressed a similar viewpoint.

Evidence from amnesic patients (e.g. McDonough, Mandler, McKee, & Squire, 1995) has shown that deferred imitation is impaired in patients with frontal lobe damage that results in impaired declarative memory. These patients are impaired in their ability to consciously recall facts and details, such as an address, but have preserved implicit learning, which allows for the storing of skills, such as the ability to re-trace the route to a particular address. This suggests that deferred imitation and explicit learning may depend on related cognitive mechanisms.

A further reason why deferred imitation may be important to comparative research is that delayed copying may rule out simple social facilitation effects (or response facilitation; see previous section on novelty). If the observer's response is not weakened by introducing a delay between demonstration and test, then it is much less likely that the effect is based on contagion, or similar excitatory processes.

It is interesting to note how few studies have set out expressly to test this aspect of imitation in animals. As can be seen in Table 2c, Bering et al. (2000) and Bjorklund et al. (2000) tested deferred imitation in chimpanzees by delaying trials by just ten minutes following demonstration (see also Bjorklund, Yunger, Bering, & Ragan, 2002). Most imitation research has used "delayed" trials, at least in the sense that trials follow demonstrations, rather than being concurrent. However, as yet the only explicit test of the effect of the length of delay on retention has been Dorrance & Zentall's (2001) experiment with Japanese quail. Using an immediate and a thirty-minute delay condition, these researchers found the same degree of behaviour

matching regardless of the delay. It remains to be seen what length of delay will result in performance deterioration, in any species.

COMPARATIVE EXPERIMENTS

Clearly, there are problems associated with comparing performance on the different task designs spread through the animal literature. The different theoretical perspectives and research questions indicated above have resulted in species being tested using very different procedures, and this has often rendered comparison somewhat meaningless. One possible solution (and one that has already been employed in several studies, as evidenced by Table 2) is to compare species using task designs that have been intentionally selected to represent as close a match possible. Within our research group we would argue that this is a very worthwhile approach, but initial attempts have been far from perfect.

It should be noted at the outset that there are considerable difficulties associated with making *any* species comparisons of cognitive ability. Bitterman (Bitterman, 1960; 1965b) in particular has discussed the problems associated with disentangling the combined effects of an individual's ability and the task's demands from the individual's performance on that task. Differences in performance could occur for a wide variety of reasons, including sensory, motor or motivational constraints. For example, a task involving visual stimuli may present a considerably greater challenge to a more olfaction-dependent species such as the rat, than it would to a predominantly visual animal, such as a primate. Bitterman (1965a) referred to such effects as "contextual variables". Bitterman suggested that valid comparisons were

nonetheless still possible, using a process of *control by systematic variation* (Bitterman, 1960), involving gradual changes to the conditions (for example, hunger levels) which might confound the detection of differences in the cognitive attribute of interest. However, MacPhail (MacPhail, 1982; 1987) has taken this reasoning further, to argue that differences in performance can virtually *always* be accounted for in terms of contextual variables. If differences are still found using systematic variation it remains possible that if such manipulations were carried to even further extremes, the differences might be eliminated. On this basis, MacPhail finds no reason to reject the “null hypothesis” that there are no differences between species in intelligence. As some authors have pointed out (e.g. Goldman-Rakic & Preuss, 1987; Kamil, 1988), MacPhail’s argument effectively prevents us from ever concluding that there might be species differences in cognition, since we can never fully rule out the possibility of “contextual variables”.

In the field of social learning, in addition to the usual obstacles associated with comparing species’ cognitive abilities, we are presented with a unique set of particular problems. The issues detailed in the following sections are ones that may be particularly challenging in social learning research.

Reward Motivation

Firstly, variation in motivational levels may play a particularly significant role in social learning research. Virtually all research into social learning has so far involved some kind of rewarded behaviour, so differences between species in levels of motivation for particular reinforcers used in social learning experiments may well

result in misleading differences in imitative performance. Dorrance & Zentall (2001), for example, have already found that showing an imitative effect in Japanese quail, *Coturnix japonica*, depended on the motivational state of the observer during the observation period. Quail were allowed to observe a trained model that received food reinforcement for producing either a pecking or a stepping response. Subjects that had been deprived of food prior to this observation tended to reproduce the particular method used by their demonstrator. However, those that had been fed prior to the demonstration showed no tendency to match the behaviour of the demonstrator. Motivational levels thus affected the tendency to imitate.

Social Interaction

Social learning experiments have also necessitated placing animals in a social situation which brings with it a new set of complications. They can lead to instances in which, despite imitative competence, animals do not perform in ways that reveal their true ability. Research to be discussed later in the thesis, using the artificial fruit methodology, suggested that olive baboons' performance was detrimentally affected by particular social contexts. For example, subordinate individuals perform less proficiently in the presence of dominant individuals (Caldwell & Whiten, 2001; and Chapter Five of this thesis). The social effects identified in baboons might confound comparisons with species with less steep hierarchies. In this respect these results are consistent with suggestions made by Coussi-Korbel & Fragaszy (1995), who suggested that socially learned traits would be more readily dispersed through populations with tolerant social structures.

There may also be different, but equally strong social effects involved in experiments using human subjects. Much of the research detailed in Table 2 has entailed comparisons of the performance of great apes with human children. In these experiments, involving demonstrations by an adult human, children may be more strongly subject to social conformity effects. These studies have found that apes are more likely to use their own, idiosyncratic methods of obtaining the task reward. However, this should not necessarily be taken as an indication that they are cognitively incapable of matching behaviours precisely. When great apes are trained to mimic novel behaviours on command (e.g. Call, 2001; Custance et al., 1995) it is clear that they *can* reproduce demonstrated actions. Thus, social conformity effects may play a role in the apparent child-ape difference. Interestingly, the conclusion of one of the studies (Tomasello et al., 1993), is that only human-raised apes may be capable of imitation. For these individuals, the subject-demonstrator relationship is likely to be more similar to that of human children, compared with the other apes.

Behavioural Propensities

Social learning research also requires overt actions on the part of the subject, another factor which contributes to the difficulties associated with making comparisons. One increasingly popular method of assessing underlying cognition within comparative psychology has been the expectancy violation procedure. This procedure, used increasingly to study cognition in human infancy, involves the recording of behavioural changes (such as looking times) as a measure of surprise when expectation is not fulfilled. "Because of the diversity of species that could be tested - all they need are eyes and an interest in visual displays - the expectancy-

violation procedure provides a powerful technique for studying what animals know” (Hauser, 2000, p61). This may well be the case for studies involving issues of cognitive representation alone, such as object permanence, concepts of number, or theory of mind. However, such approaches are of limited application for social learning research, where experiments will, by their nature, be constrained by the species’ motor abilities and confounded by their behavioural differences.

Thus performance in social learning experiments is dependent on a whole set of other variables. Many of these have been discussed by Lefebvre and colleagues (e.g. Carlier & Lefebvre, 1996; Lefebvre & Giraldeau, 1996; Lefebvre, 1995b). Traits such as neophobia, or habituation to human contact, can affect general performance in controlled experiments, and others, such as opportunism or omnivory, may be related to general learning abilities. Lefebvre suggests that species comparisons should therefore always involve a number of tasks that measure these, and that predictions about social learning should be tested on the residual deviation from regression of these potential confounds. Using this method, Lefebvre et al. (1996) found that pigeons (*Columbia livia*) were not only more rapid social learners than Zenaida doves (*Zenaida aurita*), but also solved individual learning tasks more rapidly. This led the authors to conclude that an apparent species difference in social learning could have been caused by some contextual variable, such as levels of habituation to humans.

Even when we intend to conduct comparative research using analogous procedures, true replication may be constrained by each species’ level of behavioural flexibility. In its original conception (Whiten et al., 1996) an “artificial fruit” was designed such that it could potentially be employed for studying social learning

mechanism in many species. A tool use task, for example, historically common in research in primate learning, is inappropriate for making comparisons between chimpanzees and other primates, as chimpanzees are typically much more expert tool-users than other primates.

However, although the artificial fruit methodology has now been used on several other species, significant difficulties were discovered in replicating the design with marmosets (Caldwell et al., 1999; and Chapter Three of this thesis). Marmosets lack manipulative skills possessed by many other primates tested, and as a consequence the task itself had to be simplified considerably before a marmoset demonstrator could be trained to open the apparatus. This more basic design was then used to study social learning. In comparison with chimpanzees, who have sometimes opened a fruit protected by four different defences in less than half a minute following demonstration, no marmosets succeeded in opening the artificial fruit after having observed a conspecific demonstration. Nevertheless, there was evidence that subjects matched aspects of the limited behaviours they had seen demonstrated. This raises the question of whether marmosets might have shown greater evidence of social learning if given a task that did not require as much dexterity, as suggested by the results of Bugnyar & Huber (1997) and Voelkl & Huber (2000). However, altering the task further means that analogous procedures are *not* being used. Due to the many potentially cognitively significant variables which this might affect (outlined in the section on comparative literature reviews) we should be wary of this approach.

In fact, behavioural constraints may effectively prevent us from testing in some species some of these cognitively significant aspects of imitation. For example, it is

much easier to imagine an animal with considerable manipulative flexibility (a chimpanzee or a parrot, perhaps) performing a response which we might be prepared to label “novel”, compared with those with more restricted behavioural repertoires (such as a marmoset or a pigeon). It is therefore unsurprising that some of the researchers working on these more limited species have tended to define novelty in different ways (see previous section on novelty).

Conclusions

Is a comparative psychology of social learning possible? The answer is almost certainly yes, although, like any area of comparative psychology, its conclusions are unlikely to go unchallenged. To date, comparative literature reviews have done little to clarify the picture, and often contributed to further confusion. All of the variables outlined in the section on comparative literature reviews are interesting in terms of cognitive process, and merit investigation in their own right. Only extremely rarely is a literature review published which recognizes this (e.g. see Miklosi, 1999, for a broadminded and illuminating synthesis on the possible functions of the various brands of “imitation”). Virtually all authors have tended to settle on single, preferred definitions of imitation, which may be quite different from each other, and this has led them to make different judgments about many of the same studies. Furthermore, the studies themselves are designed with often very different criteria for the kinds of social learning at stake. So when the species comparisons are made, like is rarely being compared with like.

Although presumably the results of comparative experiments will eventually be subsumed within the more global approach of an integrative review, attempts to do so in the past have been premature. Currently we need more comprehensive comparative experimentation.

How should we proceed with this? Despite the obstacles outlined in the section regarding comparative experimentation, valid comparisons can still be achieved. Firstly, lessons can be learned from other fields of comparative cognition. In response to the impracticality of judging species differences by a process of systematic variation (mentioned previously), Kamil (1988) went on to propose alternative approaches to the problem of contextual variables. He proposed that for each prediction, several experimental procedures should be designed, each testing the same ability, and that two or more species should be tested with all the procedures. If multiple predictions are fulfilled, it is unlikely that contextual variables are responsible. The example given by Kamil is of spatial memory in Clark's nutcrackers. This food-caching bird has been shown to perform better than pigeons both on a radial maze task and in a spatial operant task (cited in Kamil, 1988). Kamil (1988) also suggests that species differences could be predicted on the basis of some external criteria, and tested using a number of sample species. If the theory accurately predicts the relative performance of several species, again contextual variables are unlikely to have produced this effect. Kamil cites the example of Rumbaugh & Pate's (1984) index of encephalisation, which has been used to predict performance differences amongst seven primate species on a learning task.

In some cases, research in social learning is beginning to reach this level of rigor in terms of the comparisons made. For example, as can be seen from tables 2a and 2b, there are now several studies (Call & Tomasello, 1995; Nagell et al., 1993; Whiten & Custance, 1996) involving comparisons between chimpanzees and children, all of which converge on a conclusion that there are systematic differences in performance between these two groups. It appears that, whilst young children typically copy with a high degree of fidelity, chimpanzees often employ their own idiosyncratic techniques. These results can now be used to generate operational predictions about the circumstances under which each of these groups will tend to show high levels of fidelity (Whiten et al., in press). Above all, it is important that we begin to make directional and predictive hypotheses about species differences, rather than correlational and postdictive ones. The different theories of the species distribution of imitation should be employed in terms of forming operational criteria against which to test predictions for a number of species.

As was noted previously, sometimes it is impossible to fully replicate a task with a different species. However, in situations where subjects' capabilities necessitate modifying a task design, attempts should be made as far as possible to retain aspects of the procedure that may be cognitively significant.

Since each of these cognitively significant variables are interesting in their own right, teasing them apart with a variety of different task designs may prove to be the most rewarding approach. This should provide a more complete understanding of social learning abilities, and may also enlighten debate on the origins of imitation, as

we may find that certain forms of “imitation”, and other forms of social learning, show very different patterns of species distribution.

Finally, the number of researchers beginning to study social learning in a number of diverse species is encouraging. In order to truly evaluate the nature of the phylogenetic distribution of imitation, researchers must be prepared to branch out from their familiar study species. The rats and pigeons studied by researchers from the animal model perspective will tell us little in isolation, and the same is true of the great apes favoured by those working from the phylogenetic perspective. Only through a truly integrative research program can we hope to challenge some of the assumptions of the traditional disciplines (whether those of comparative psychology, behaviourism or ethology), and forge a coherent comparative psychology of social learning.

Chapter Three

SOCIAL LEARNING OF AN ARTIFICIAL FORAGING TASK IN COMMON MARMOSETS

As detailed in the previous chapter, the use of analogous tasks is a powerful method of comparing species' social learning abilities. The present chapter describes work cited in the previous chapter, and published in Caldwell et al. (1999) using the artificial fruit methodology to test for imitative learning in common marmosets.

Common marmosets are a New World monkey species, from the family *Callitrichidae*, which is made up of marmosets and tamarins. Callitrichids are known for their co-operative social organisation, usually involving a dominant pair, both of whom breed, and a number of adult offspring that contribute to the care of infants (e.g. Rothe & Darms, 1993; Stevenson & Rylands, 1988). The particular species studied in this chapter, *Callithrix jacchus*, show this typical social pattern. Common marmosets occur in the Atlantic coastal forests and dry thorn scrub of northeast Brazil, and are described as, "highly gummivorous", feeding mainly from exudate gouged from tree trunks and branches, as well as fruit and insects (Rylands & de Faria, 1993).

As noted in the previous chapters, even within the hotly debated field of nonhuman imitation, *particular* doubt has been cast on whether monkeys are capable of imitation. Visalberghi & Fragaszy (1990), in their article "Do monkeys ape?", conclude that, "Monkeys do not seem to be capable under common circumstances of

learning tool use by imitation” (p269). They also state that the social processes that lead to rapid cultural learning in humans, “may be completely absent in monkeys.” (Visalberghi & Fragaszy, 1990, p269). Furthermore, Whiten & Ham (1992) concluded that imitation was unproven in monkeys, whilst judging that great apes, in contrast, “share with humans an imitative capacity” (p276).

However in some respects, marmosets may represent likely candidates for showing imitative ability. According to the adaptational perspective, there are good reasons why they might have developed imitative tendencies, living as they do in co-operative extended family groups. An imitative capacity might provide valuable shortcuts to learning about the environment. General process theories of imitation would make similar predictions for marmosets. Given that they are accustomed to foraging non-aggressively in groups, they are liable to gain large amounts of experience of synchronous behaviours. Thus a stimulus generalisation model would predict that they would be likely imitators.

Furthermore, the tolerant nature of callithrichid social dynamics may provide the ideal conditions for an imitative capacity to be expressed. Some authors have argued that although evidence for imitation in monkeys is weak, this may be due to the social constraints of hierarchical group structures (Fragaszy & Visalberghi, 1989; Visalberghi & Fragaszy, 1990). Thus, in previous research on social learning in monkeys, learning may have been inhibited because more dominant individuals exploit, rather than learn from, skilled subordinates; and subordinates are inhibited from approaching, and therefore learning from, skilled dominant individuals. However, such constraints are less likely to operate within a marmoset family group.

In addition to the co-operative breeding system, the level of food sharing observed within callitrichid family groups is noteworthy. Tardif, Harrison, & Simek (1993) have stated that, “Callitrichids are unique amongst primates in the degree to which group members provide solid food to youngsters” (p231). In a review of callitrichid cognition, Snowdon (2001) has suggested that such tolerant social interactions make these species the ideal models for research into social learning and imitation.

Imitation has previously been investigated in marmosets by Bugnyar & Huber (1997) and Voelkl & Huber (2000). In the former study, marmosets were provided with a pendulum door that could be either pushed or pulled to gain access to a food reward. These researchers allowed observer monkeys to watch a demonstrator monkey pulling open the door. Some observer monkeys showed a stronger tendency to use the demonstrated opening technique than control (non-observer) monkeys, whose natural response was to push the door.

However, as can be seen from Table 1 in the previous chapter, some authors have argued that this particular study does not provide adequate evidence of imitation. Heyes & Ray (2000) describe the result as “suggestive, but not conclusive, evidence” of imitation (p232). And Zentall (2001) makes a more specific criticism about the methodology, pointing out that only one of the two groups of subjects actually saw a demonstration. Bugnyar & Huber (1997) describe their methodology as a two-action design, but the design is only two-action in the sense that the manipulandum itself can be operated two different ways, not in terms of there being two different observer groups that each see one of these methods demonstrated (as has been done in other “two-action” studies, such as those carried out by Akins & Zentall (1996), Whiten et

al. (1996) and Zentall et al. (1996)). There were therefore important differences between the two groups that might potentially account for the difference in subjects' subsequent behaviour. The "push" group had seen no demonstrator. In fact they were not provided with any kind of pre-test observation period, so not only had they not seen a conspecific operate the apparatus, they had never seen it at all before. Subjects from this group therefore came to the task entirely 'cold'. Their behaviour was clearly affected by this, as evidenced by the finding that subjects in this group were more exploratory than those that had seen the demonstration. The difference in their operation of the door may have arisen for a similar reason.

More recently, however, Voelkl & Huber (2000) addressed such criticisms. Their task involved opening photographic film canisters, and two trained demonstrators were used, one of which removed the lid with their hand, and another which used their mouth. Voelkl & Huber (2000) found a significant difference between the two observer groups in the method used to open the canisters: those subjects that saw the hand method all used their hands every time, and of the subjects that saw the mouth method, most used their mouth for at least some of the test trials. Voelkl & Huber (2000) therefore presented their results as evidence of "true imitation", as the difference could be attributed to neither stimulus enhancement nor emulation.

The purpose of the current study was therefore to investigate imitation in marmosets further, using the artificial fruit methodology. The artificial fruit (as used by Whiten et al., 1996) is a box locked by several defences, each of which can be operated in two alternative ways. It is designed to represent an ecologically valid test

for imitation, in that a certain amount of manipulation is required before the edible “core” (a food reward inside) can be reached. The artificial fruit is therefore a slightly more complex task than that employed by Voelkl & Huber (2000), as a combination of actions are involved. Success on this task is therefore less likely to be dismissed by critics such as Byrne (Byrne, 2002; Byrne & Russon, 1998) as a case of “response facilitation”. Furthermore, Huber et al. (2001) have also suggested that the artificial fruit is the ideal methodology for showing how the investigative behaviours of explorative species may be influenced by observation of a demonstrator. The combinations of complex manipulations allow for the analysis of exploratory responses in a way that tasks involving minimal manipulations of simple objects cannot.

The primary aim was therefore to train two conspecific demonstrators to manipulate a marmoset-sized version of the artificial fruit in order to investigate whether observers produced demonstrator-consistent responses, indicative of imitative ability. A further goal was to investigate whether success levels in these observer groups were greater than those for a third, non-exposed control group, which would suggest that social learning generally played a functional role in terms of enhancing performance on this particular task.

Study One

TESTING FOR SOCIAL LEARNING AND IMITATION IN *CALLITHRIX JACCHUS* USING AN “ARTIFICIAL FRUIT”

METHODS

Subjects

Fourteen marmoset (*Callithrix jacchus*) subjects were involved in this study: eight females, and six males. These included juvenile, subadult and adult animals, ranging in age from six months to seven years old. Of these animals, 12 were subjects in the study, and two were trained as demonstrators. The animals were drawn from the breeding colony of a population of animals housed in a Medical Research Council facility. None had been subjected to any invasive research. They were housed in family groups of between three and eight individuals with similar group structure to wild common marmosets (see introduction). All animals came from a total of 3 of these family groups and all testing was done within the family group, so that subject and demonstrator came from the same home cage. Figure 1 depicts the layout of the home cages. All cages were 230cm(h) x 110cm(d) x 120cm(w) and were equipped with branches, ropes and platforms. All animals were fed a diet of fruit, commercial marmoset food, and protein and vitamin supplements, with water supplied ad libitum.

Figure 1. – The marmoset home cages, in which testing was carried out

The cages can be divided into four sections (top left, top right, bottom left, bottom right). During testing subjects and demonstrators were sectioned off from their other group members by opaque plastic cage dividers.

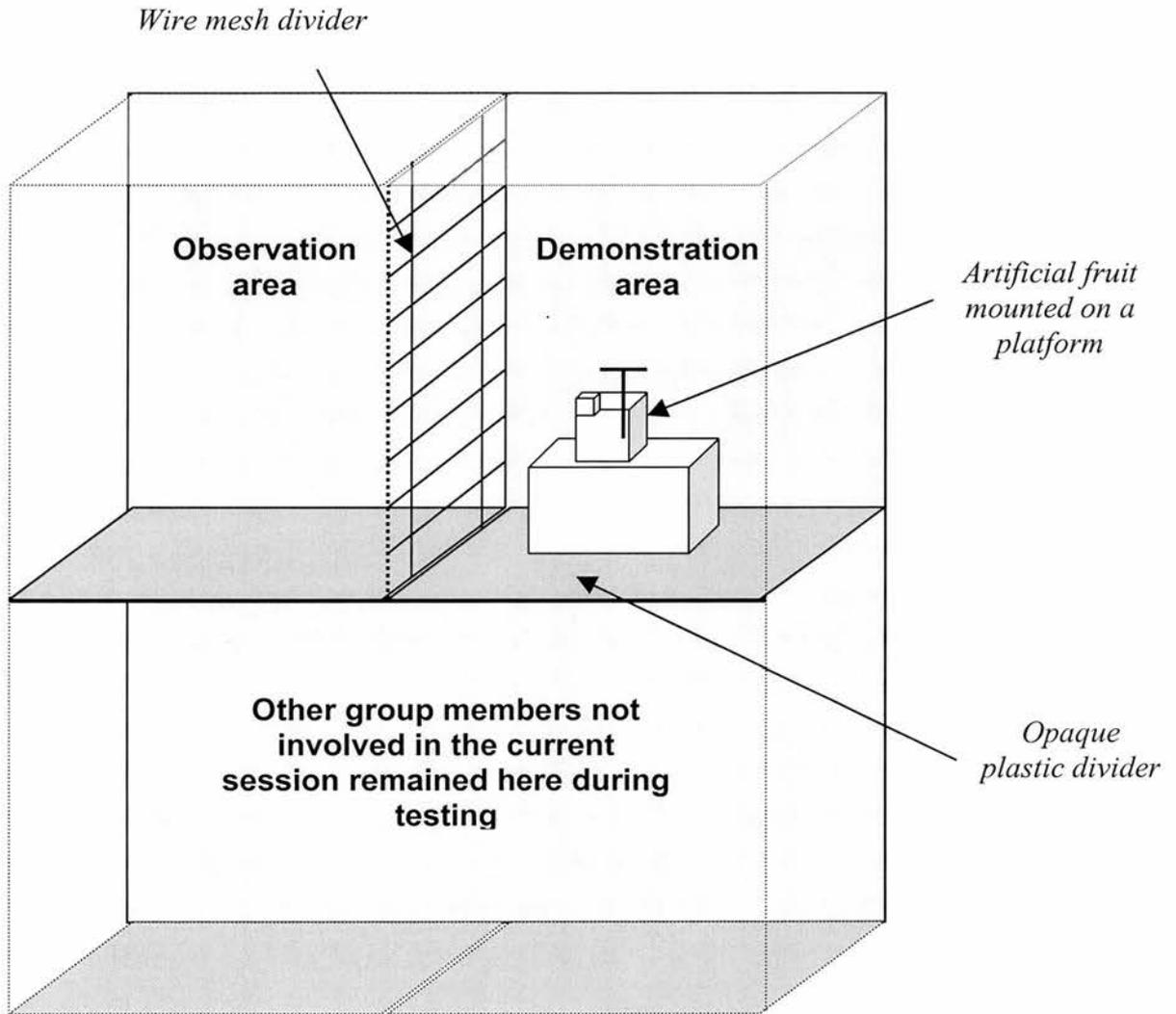
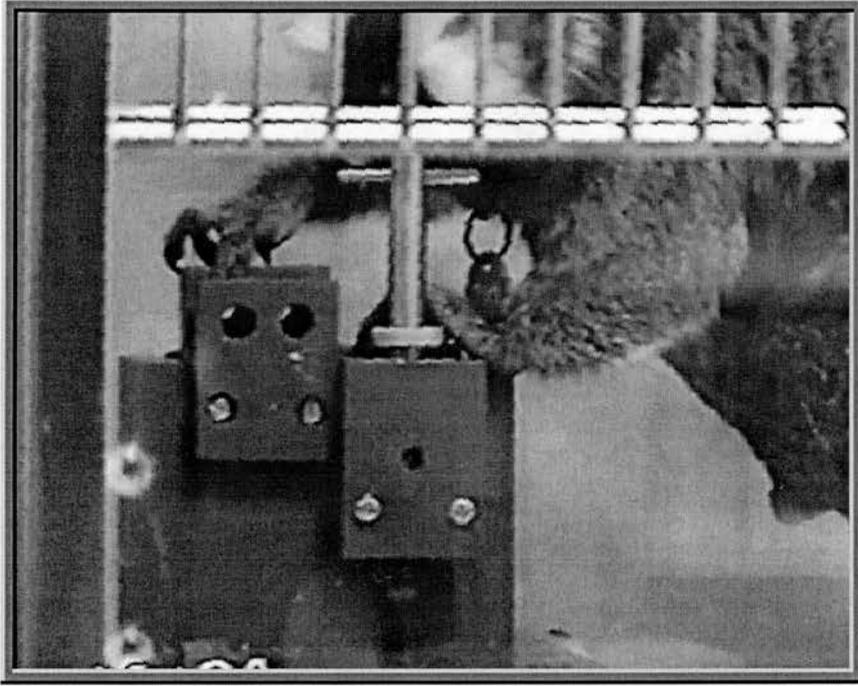


Figure 2. - The marmoset artificial fruit, operated by the demonstrator for the “Hand” group



Apparatus

The task employed was an “artificial fruit”, of the kind used by Whiten et al. (1996) to test for imitation in chimpanzees. The version used in this study was a much smaller one, designed for manipulation by small monkeys (6x6x8cm). Only one of the original defenses was used, due to the limited manipulative abilities of marmosets (see next section for details of how a demonstrator was trained on this defense). Figure 2 shows the artificial fruit used in this study, which was a box locked by a handle which must be removed to release a lid and gain access to the enclosed food reward.

Training and Habituation

Each of the demonstrators was the breeding female of her group. Training of the demonstrators was done in the home cage, with the animal isolated from the rest of the group members. Only one demonstrator was successfully trained to open the artificial fruit. This individual turned the handle from the bottom and lifted the lid by pulling it up (see Fig. 2) from the bolt-holes (N.B. Although no bolts were used in this study, the artificial fruit still had bolt-holes, being based on the design used in Whiten et al., 1996). However, in order that there were still two comparable conditions each involving a conspecific interacting with (and gaining a food reward from) the artificial fruit, another was shaped to eat food from the outside of the box.

Shaping of the “Hand” demonstrator, who opened the artificial fruit, took place over several weeks. She was initially allowed to remove food from inside the artificial fruit with the lid open. Over subsequent sessions, the lid was closed further until the demonstrator could access the food reward from the artificial fruit with the lid fully

closed. Following this, the handle was added, initially only slightly overlapping the lid, such that it did not need to be moved far to free the lid. Over several more sessions the demonstrator became able to access the food reward with the handle in the fully locked position. Despite a variety of approaches towards training this individual to remove the bolts (including placing them only part-way in, and replacing the metal bolts with bolts constructed from carrot and hard fruits), she never succeeded in removing this defense. Food rewards were varied in accordance with the demonstrator's apparent motivation for them. Chopped banana was used, as was chopped grape, and occasionally raisins. These were items which were included in the animals' daily diet, but they were known to be preferred food items within the diet. Training was generally carried out before lunchtime, when the animals received their daily feed.

Shaping of the other ("Mouth") demonstrator was more straightforward as she was only required to eat food from the lid of the apparatus. However, she was introduced to the artificial fruit and allowed to eat from it on several occasions, until she was regularly approaching and eating from the apparatus whenever she was isolated with it. The food reward used in this case was mashed banana.

Procedure

Each subject received four trials, each consisting of an observation phase followed by a test phase. Due to the way in which the home cage could be divided up (into four equally sized sections), trials would commence when the required combination of individuals from the group had entered the top two sections (see Fig.

1). The artificial fruit was then introduced and the observation phase began. During the observation phase for the first three trials the demonstrator performed (opening the artificial fruit at least three times and removing chopped banana from the inside for the hand group; eating mashed banana from the lid of the artificial fruit for the mouth group), and the subject could observe this from the other side of a wire mesh divider (see Fig. 1). The experimenter reached into the cage several times during each observation phase in order to reload the artificial fruit when the demonstrator had removed all of the food. For the hand demonstrator this also involved re-locking the artificial fruit. The control group were also allowed to view the apparatus through the wire mesh, although no demonstration was performed. In each subject's fourth trial, an "interactive" observation phase was introduced. Demonstrations given were the same for each of the groups, but subjects were not separated from the demonstrator. Those in the hand and mouth groups were therefore able to interact with their demonstrator and share the food rewards. The control group were simply given extra time to interact with the apparatus alone. Each observation phase took five minutes (including reloading time), after which the demonstrator was released into another section of the cage to rejoin the rest of the group (see Fig. 1). In between each observation and test phase, the outside of the artificial fruit was wiped clean of any residual food. During the test phase the subject was isolated with the artificial fruit for five minutes. All trials were videotaped for later analysis, including observation and test phases.

Data Coding

Independent coders were instructed to record the behaviour of the subjects during the test phases, using the coding sheet shown in Appendix I. For each of the

points listed on the coding sheet, they recorded the number of touches to the artificial fruit that the subject made. Since these were divided into specific parts of the artificial fruit, and also the body part used (hand or mouth), it was expected that these data could be used to identify whether the subjects were showing demonstration-consistent behaviours.

RESULTS

Overall Performance and Success

None of the subjects from any of the groups succeeded in opening the artificial fruit and gaining the food reward, a result which contrasts strongly with those found with other primates that have been tested using this methodology. This issue will be returned to in the discussion. It was still possible however to investigate whether social learning had an effect on the subsequent performance of the subjects. The totals reported for each of the coding categories were lumped for each subject, in order to determine whether there were any differences between the three groups in terms of the amount of exploration and manipulation that occurred during trials.

It was found that there was a difference between the three groups in the amount of overall touches they made to the artificial fruit over the four trials. Each of the coding categories shown on the sheet in Appendix I was collapsed for each subject over the four trials to give the total number of touches they made. A one-way analysis of variance showed there was a difference between the three demonstration groups in the total number of touches made (ANOVA: $F_{2,9} = 10.578$, $P < 0.005$). Post-hoc tests showed that there were significant differences between the hand and control group

(LSD: $P < 0.001$) and the mouth and control group (LSD: $P < 0.05$), but not between the hand and mouth group (LSD: *NS*).

Body Part Copying

In order to determine whether subjects copied the body part used by the demonstrator, totals were calculated for the number of hand touches and mouth touches each subject had made over the four trials. A repeated measures analysis of variance (three-by-two) showed a significant interaction between the number of touches made with hand versus mouth and the type of demonstration seen (ANOVA: $F_{2,9} = 4.369$, $P < 0.05$), which is illustrated in Fig. 3. There was also a main effect of group (ANOVA: $F_{2,9} = 10.578$, $P < 0.005$), as reported in the one-way analysis by group given above. There was no main effect of body part preferred, however (ANOVA: $F_{1,9} = 4.236$, *NS*). Further analysis of two-by-two interactions showed that there was an interaction between the hand and mouth groups on these measures (ANOVA: $F_{1,6} = 6.013$, $P < 0.05$). Thus, those individuals that saw the “Hand” demonstration, did make proportionally more hand touches, and those that saw the “Mouth” demonstration, made proportionally more mouth touches. There was also a significant interaction between the hand and control group (ANOVA: $F_{1,6} = 9.426$, $P < 0.05$), but no interaction between the mouth group and the control group (ANOVA: $F_{1,6} = 0.655$, *NS*).

Figure 3. - Total hand and mouth touches (over four trials) to the artificial fruit for Hand, Mouth and Control groups (mean +/- standard error)

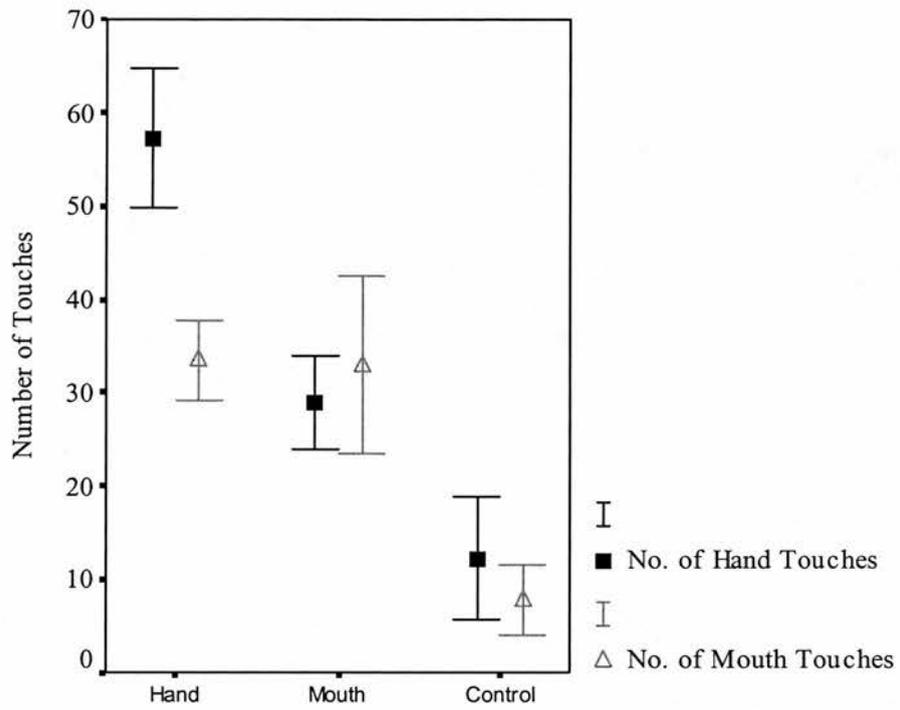
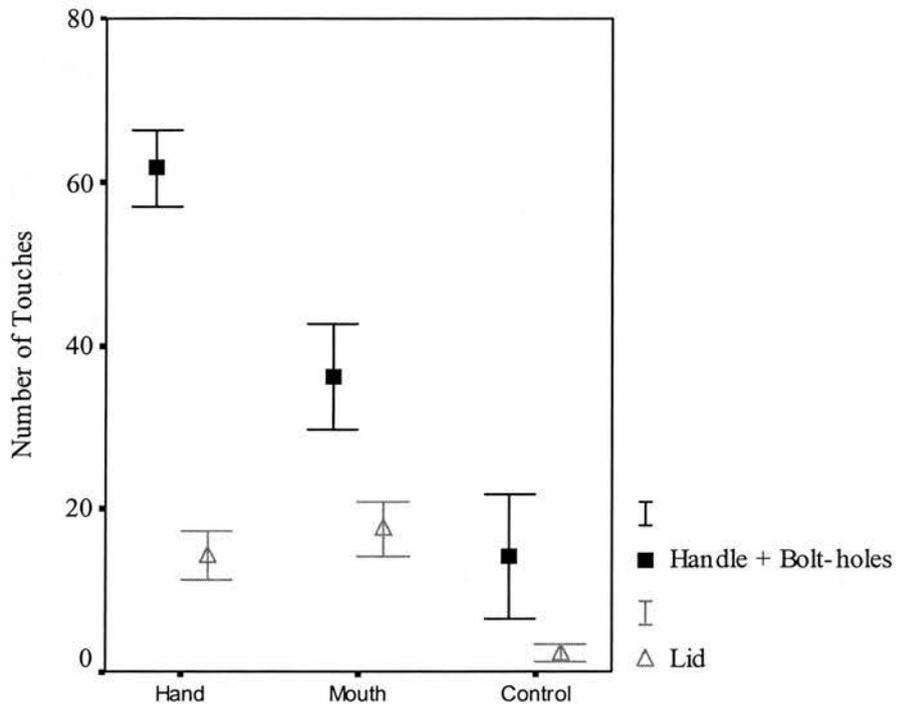


Figure 4. - Total touches to handle plus bolt-holes and to lid (over four trials) of the artificial fruit for Hand, Mouth and Control groups (mean +/- standard error)



These interactions involving the control group ought to be treated with a certain level of caution however. Due to the extremely low levels of responding of this group, interactions (or lack of such) between this groups' pattern of responses and those of the other groups could occur as an artefact of floor effects of this group. However, one-way analysis of the absolute number of touches for both hand and mouth appear to corroborate these interactions, as will be argued in further depth in the discussion. There was an effect of group on the number of hand touches made (ANOVA: $F_{2,9} = 12.553$, $P < 0.005$), and post-hoc testing showed that the hand group made significantly more hand touches than both the control group (LSD: $P < 0.001$) and the mouth group (LSD: $P < 0.05$). The mouth group and the control group were not significantly different on this measure however (LSD: NS). Mouth touches were also related to group (ANOVA: $F_{2,9} = 5.191$, $P < 0.05$), and both the hand group (LSD: $P < 0.05$) and the mouth group (LSD: $P < 0.05$) made more mouth touches than the control group. However, the hand and mouth groups were not significantly different from each other (LSD: NS).

Place Copying

Demonstrator-consistent effects of the specific areas of the artificial fruit explored by subjects were also investigated. The "Hand" model had turned the handle and lifted the lid using the bolt-holes. It was therefore predicted that the observers from this group would concentrate on these areas more, compared with the mouth group. The mouth group, in contrast, had seen their demonstrator lick the lid of the artificial fruit, so it was expected that they would show a greater focus on this particular area. Again, the data provided by the independent coders was collapsed in

such a way that each subject was given a total number of touches for the lid, and for the handle and bolt-holes. A significant interaction (three-by-two) was found between these measures and the demonstration seen (ANOVA: $F_{2,9} = 13.731, P < 0.005$). This is illustrated in Figure 4. There was also a main effect of place, with the handle and bolt-holes being touched more overall than the lid (ANOVA: $F_{1,9} = 78.859, P < 0.001$), and a main effect of group, consistent with the one-way analysis of total touches (ANOVA: $F_{2,9} = 12.985, P < 0.005$). Again, further two-by-two analyses of the interactions isolated differences between the hand and mouth group (ANOVA: $F_{1,6} = 24.689, P < 0.005$). This was consistent with a prediction of demonstration-consistent responding as the hand group were contacting handle and bolt-holes proportionally more, and the mouth group were contacting the lid proportionally more. There was also a significant interaction between the hand group and the control group (ANOVA: $F_{2,9} = 25.247, P < 0.005$) but not between the mouth group and the control group (ANOVA: $F_{2,9} = 0.037, NS$).

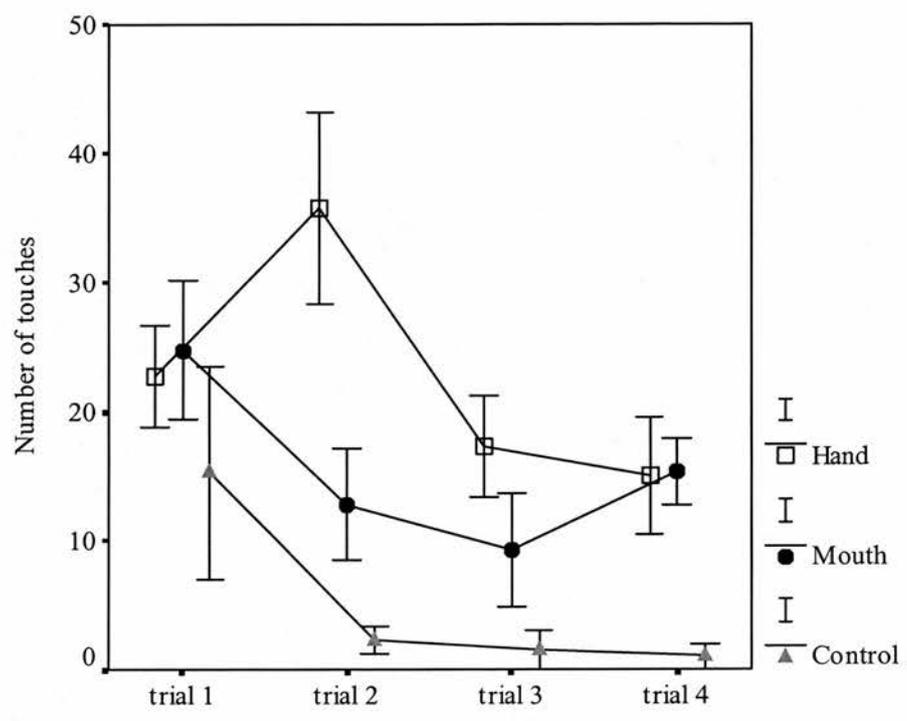
As mentioned in the previous section, the low levels of responding by the control group mean that the interactions involving this group must be treated with a certain amount of scepticism. However, once again, one-way analyses of the absolute values for handle plus bolt-holes and lid appear to back up these results. There was an effect of group on the number of touches made to the handle and bolt-holes (ANOVA: $F_{2,9} = 13.836, P < 0.005$), and post-hoc testing showed that both the hand group (LSD: $P < 0.001$) and the mouth group (LSD: $P < 0.05$) made significantly more touches than the control group. The hand group also made significantly more touches to the handle and bolt-holes than the mouth group (LSD: $P < 0.05$). Lid touches were also related to group (ANOVA: $F_{2,9} = 9.347, P < 0.01$), and both the hand group (LSD: $P < 0.01$) and

the mouth group (LSD: $P < 0.005$) made more lid touches than the control group. However, the hand and mouth groups were not significantly different from each other (LSD: *NS*).

Analysis over Trials

Each subject was given four trials, including an observation period and a test period, as described in the methods section. It was expected that there would be a gradual decrease of interest in the artificial fruit over these trials, due to a habituation effect. The total number of touches was calculated for each subject for each trial which permitted a trend analysis, which showed that there was a decrease in subjects' activity over trials (Pages's *L* Trend test: $L_{4,12} = 321$, $P < 0.05$). However, as can be seen from Fig. 5, there was no drop off in performance between trials 3 and 4, contrary to the general pattern. As was mentioned in the methods section, the fourth trial included an "interactive" demonstration, in which subjects from both the hand and mouth group were not separated from the demonstrator, and could therefore interact and share food rewards with them. Although it is an extremely speculative conclusion, it is possible that this condition may have renewed subjects' interest in the apparatus. This issue will be addressed further in the discussion, and also in later experiments presented in the thesis.

Figure 5. - Number of touches to the artificial fruit for trials 1, 2, 3 and 4 for Hand, Mouth and Control group (mean +/- standard error)



DISCUSSION

Imitative effects

In contrast with results found with chimpanzees (Whiten, 1998; Whiten et al., 1996), capuchin monkeys (Custance et al., 1999), gorillas (Stoinski et al., 2001), and orang-utans (Custance et al., 2001), none of the marmoset subjects succeeded in opening the artificial fruit during any of their trials. These differences in manipulative competence, in combination with the slight differences in design and task complexity, meant that unfortunately it was not possible to directly compare the performance of the marmosets with these other primates. Such obstacles to meaningful comparison were discussed in the previous chapter.

However, there was definite evidence of demonstration-consistent responding in the subjects, both in terms of the body part they preferred for exploration of the artificial fruit, and the areas on which they concentrated. Particularly noteworthy with regard to the issue of imitation is the reproduction of the part of the body used. Animals who watched predominantly mouthing behaviours used their mouths more, and those who watched predominantly manipulation used their hands more. This effect is logically similar to results reported by Zentall with pigeons and quail (Akins & Zentall, 1998; Zentall et al., 1996) mentioned in the previous chapter, and those reported by Voelkl & Huber (2000), also studying marmosets, each of which has been labelled “true imitation”.

This result should be interpreted with caution, however. As Kaiser, Zentall, & Galef (1997) and Zentall (2001) have pointed out, conclusive evidence of imitation

(as opposed to a combination of a number of other social learning effects; in particular stimulus enhancement, contagion and emulation) on a two-action test is only shown when the frequency of *both* of the demonstrated behaviours is increased in the respective observer groups, compared with a non-exposed control group. In the study reported here, the overall level of interest in the artificial fruit was higher for the mouth group, compared with controls, but there was no interaction in terms of the relative number of hand and mouth responses. As noted in the results section, this result could possibly have arisen as an artefact of floor effects within the control group. However, analysis of the absolute number of hand and mouth responses appear to support the interpretation that the mouth group were not influenced in their *specific* behaviours towards the artificial fruit compared with the controls. The hand group showed more hand touches than both the mouth and control groups, but the mouth group, although showing a greater number of mouth touches compared with controls, did not show a greater number of mouth touches than the hand group.

The higher level of responses overall could easily be attributed to a stimulus enhancement effect as a result of having seen a conspecific interacting with the apparatus and receive a reward. However, since mouthing responses in particular did not appear to be facilitated in this group, they may not have been influenced by the actual actions performed by the model. This then leaves open the possibility that the increased use of the hand to manipulate the artificial fruit in the hand group was not an imitative effect, but dependent on any one (or a combination) of several other social learning effects. For instance, it may be the case that reaching or grasping behaviours are in some way contagious in marmosets, an interpretation Byrne (Byrne & Russon, 1998; Byrne, 2002) would label “response facilitation”. However, a more

likely interpretation may be that the marmosets from the hand demonstration group learned something about the task that the other two groups did not, which motivated them to attempt to open the artificial fruit (a motivation which entailed the use of the hand).

Non-Imitative Social Learning

It may be the case therefore that the marmosets from the hand group showed what Huber et al. (2001) have labelled a *motivational* effect of the demonstration. A study by Palameta & Lefebvre (1985) is noteworthy in this regard. Pigeon subjects were presented with a food-finding task which required that they peck through a paper lid. Birds that observed the full demonstration were more successful than both of the control groups, one of which saw only the pecking and no reward, and one of which saw the demonstrator eat through a ready-pierced lid. This latter condition is perhaps comparable with the group that saw the mouthing demonstrator in this chapter. This group saw no actual manipulation of the artificial fruit, as the demonstrator's food reward had been on the outside. These animals showed a corresponding reduction in manual exploration of the artificial fruit compared with those that saw the full demonstration.

Consistent with this interpretation, the motivation levels of the hand group did not tail off quite as rapidly as those of the other groups and, as can be seen from Fig. 5, they actually increased quite dramatically between trials one and two. This would suggest that, despite being unable to access the food reward, subjects from this group persisted in their attempts, unlike those from the other two groups.

Perhaps the most striking result of the study is the finding that observers specifically focussed on the areas of the apparatus that the demonstrator had contacted. There was a clear difference between the hand group and the other two groups in terms of where they directed their touches. This effect could be interpreted as a case of very *localised* stimulus enhancement (compared with a general stimulus enhancement effect would account for the difference in total touches between the hand and mouth groups compared with the control group). The only other study to identify such an effect is Huber et al.'s (2001) artificial fruit experiment with keas. Closer inspection of the present results also suggests that once again the hand group in particular gained valuable information about the task from watching the full demonstration. Again, it was the case that although there was a significant interaction between place of touch (to handle and bolt-holes compared with lid) between the hand group and the mouth group, an interaction was not found between the mouth and control group. Furthermore, analyses of the absolute number of touches again showed that although the hand group appeared to be selectively facilitated towards the handle and bolt-holes (as compared with the other two groups), there was no such effect for the mouth group on the lid. Therefore, it appears that the hand group learned from the demonstration which specific parts of the artificial fruit should be manipulated. Such effects could potentially form a very powerful drive in social learning, without actually requiring imitation. If individuals are drawn to the functionally relevant parts of an object following observation of a demonstration, then this will certainly move them more quickly towards finding solutions.

As mentioned in the results section, Figure 5 highlights a further interesting result which was the performance of the two observer groups on the fourth trial,

which may have indicated a renewed interest in the apparatus (or at least a slowing down of the habituation effect). As noted in the results section, this occurred when subjects were given an “interactive” demonstration session during which they could share the food reward gained by the model. What makes this result of particular note is that in the previous literature, such interactive demonstrations have typically been associated with a *drop* in the performance of subjects during subsequent testing (e.g. Giraldeau & Lefebvre, 1987). Thus scrounging food rewards from a trained demonstrator has generally been considered to have an inhibiting effect on social learning. From the current results it appears that, under certain circumstances at least, marmosets do not follow this general pattern. This issue will be investigated further in the following chapter.

Conclusions

In conclusion, therefore, subjects clearly gained a lot of information from observing demonstrations. There was evidence of demonstration-consistent responding, in terms of both the body part used, and the parts of the apparatus that were contacted. However, this does not represent conclusive evidence of imitation.

Social learning in a more general sense clearly influenced the behaviour of the subjects however. The non-observer control group showed much lower levels of general exploration of the artificial fruit. This is an important result from a practical perspective. Custance et al. (2002), in their review of the relevance of social learning to primate reintroduction, note that it is important to compare demonstration groups with non-exposed controls in order to determine whether social learning confers any

real benefit to the animal. The results of this study would suggest that demonstrations may benefit observers in many different ways. In addition to the difference between control and observer groups, there were also important behavioural differences between subjects from the hand group (that saw the complete demonstration) and those from the mouth group. Individuals from the hand group had the highest success rate in that not only were they making the most touches of all of the groups, but they were also using their hands relatively more and directing their touches to the relevant locations.

It is interesting that, despite the obvious difficulty (near impossibility) of this task for the marmosets, these clear differences between the groups were found, highlighting some fairly complex social learning. This supports the point made by Huber et al. (2001) that difficult tasks such as the artificial fruit may be very useful for identifying a variety of (not necessarily imitative) social learning effects on exploratory actions.

Difficult tasks such as the one presented here may also be preferable for identifying the practical benefits of social learning. Despite finding evidence for imitation, Voelkl & Huber (2000) initially found no actual benefit to observer animals in terms of success rate, as control animals opened just as many canisters. However, when the task was made more difficult by closing the lid of the canisters much more firmly, they found a large difference in success rate between one of their demonstration groups and the non-observers. Social learning may in fact provide the greatest practical benefit to individuals when it increases the motivation to persist

with unrewarded manipulations of an object (or specific parts of that object), as individual learning alone is unlikely to be successful under such circumstances.

Chapter Four

SOCIAL INTERACTION AND SOCIAL LEARNING IN COMMON MARMOSETS

In the previous chapter, it appeared that being able to interact with and share a food reward with a trained demonstrator did not inhibit a marmoset observer's motivation or performance. Since this presents an apparent contrast between the marmosets and many other species studied, this suggests that social contexts could differentially affect the performance of different species. As discussed in Chapter Two, this is highly relevant to making species comparisons of social learning ability. This chapter therefore presents material from Caldwell & Whiten (in press-b), the aim of which was to investigate further the effect of close social interaction on social learning in common marmosets.

In the literature on social learning, somewhat contradictory expectations exist with regard to the effect of social interaction on the tendency to learn a demonstrated behaviour. Whilst it is often assumed that information will spread in a non-random way through a population, mediated by social relationships that permit joint interaction (e.g. Kawai, 1965), experimental research has tended to view close social interaction as a potential *obstacle* to social learning, the standard experimental paradigm therefore incorporating some kind of physical separation (such as wire mesh) between the skilled and naïve individual (e.g. Bugnyar & Huber, 1997). This type of design is generally considered to be beneficial to the study of social learning, as allowing the two animals to interact can lead to scrounging by the naïve individual,

which is generally described as having an inhibiting effect on learning (e.g. Frigaszy & Visalberghi, 1989; Beauchamp & Kacelnik, 1991).

There are two main reasons why scrounging is generally supposed to have an inhibitory effect on learning. The first is simply that what the naïve individual is learning is *to scrounge*, as opposed to learning the new skill. So for example, the presence of the skilled individual could be being used as a cue, overshadowing the learning of cues relevant to the task (e.g. Beauchamp & Kacelnik, 1991), or reinforcement may be more reliably obtained by following a skilled individual, as opposed to interacting with the task itself (e.g. Giraldeau & Lefebvre, 1987). Secondly, scrounging and learning have been viewed as mutually exclusive strategic options determined by the relative payoffs involved (e.g. Barnard & Sibly, 1981; Fritz & Kotrschal, 1999a; Giraldeau & Caraco, 2000).

Experimental tests that have explicitly compared pure observation of a trained demonstrator with scrounging from a trained demonstrator have tended to support this view. Nicol & Pope (1994) investigated social learning in chickens and compared a “free” condition in which demonstrator and observers could interact, with a “screen” condition in which they could not, and found that observers that had been separated from the demonstrator subsequently performed the task more successfully than those that had been able to interact. Giraldeau & Lefebvre (1987), studying pigeons, compared a condition which allowed observers to share the reward obtained by a demonstrator with a purely observational demonstration. They found that pigeons that had received the scrounging demonstration performed no better than a no-demonstration control group during subsequent tests.

However, there are also good reasons why being able to interact jointly with a skilled demonstrator might facilitate a naïve observer's acquisition. Social support may reduce neophobic responses, thereby facilitating interaction with and exploration of novel objects. Very close social interaction with the demonstrator may also allow the observer to perceive in greater detail crucial skill-related actions. Finally, if scrounging itself entails a certain amount of interaction with the object or apparatus involved, it may mediate a significant degree of individual learning (e.g. learning the connection between the apparatus and reward).

Indeed, in some cases where model and observer have been allowed to interact, it has been noted that scrounging has not necessarily prevented the transmission of a new behaviour (e.g. Fritz & Kotrschal, 1999b). Furthermore, Midford, Hailman, & Woolfenden (2000) explicitly compared a "scrounging enabled" condition, where food could be shared by naïve observers with a "scrounging restricted" condition in which the demonstrator could monopolise the reward. Their scrub jay subjects showed more effective learning when scrounging was possible. However, the authors note that the manipulation used (several small pieces of food vs. one large piece) significantly altered the behaviour of demonstrators in such a way that they could not rule this out as the source of the variation between the groups. The single large reward tended to result in the demonstrators spending a much shorter period of time performing the behaviour to be learned (digging in a specific target area).

Therefore, to date, there has been no conclusive evidence of the facilitating effect of social interaction, compared with pure observation, on social learning in any species. However, it was expected that if scrounging was studied within a population

characterised by tolerant social interactions, this effect might be found. Terkel (1996) described experiments on the social transmission of pine cone feeding amongst black rats, and showed that rat pups would readily adopt the skill if their mother displayed it. Conversely, naïve animals housed with unrelated demonstrators (even for months at a time) failed to develop the behaviour. Learning to strip the pine cones required a certain amount of interaction with partially processed cones, and since rats do not generally tolerate the proximity of other rats during feeding, this was never possible when unrelated individuals were paired. Pups could learn from their mothers, however, because their presence (and thieving of partially stripped cones) was tolerated.

Common marmosets were studied here, a species that has already shown evidence of social learning (Bugnyar & Huber, 1997; Caldwell et al., 1999; Voelkl & Huber, 2000). This species were also expected to show the kinds of tolerant interactions necessary to observe a facilitative effect of scrounging. As noted in the previous chapter, common marmosets live in family groups in which typically one female breeds and other group members contribute to the care of infants (Rylands & de Faria, 1993). Food sharing has also been documented in several marmoset species, including common marmosets (Feistner & Price, 1991).

There were two main aims to this study. The primary question was whether social interaction with a skilled partner would facilitate learning compared with the standard dual-cage procedure. Secondly, the study was designed to test whether any such effect could be attributed to the increased opportunity for individual learning

about the apparatus, and/or to increased interaction with the apparatus due to the social support of the presence of a conspecific.

Study Two

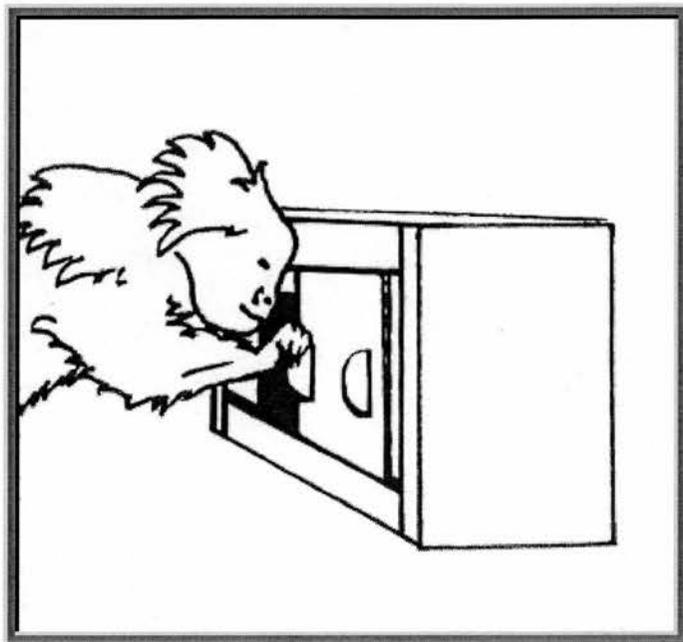
THE EFFECT OF SCROUNGING ON SOCIAL LEARNING IN *CALLITHRIX JACCHUS*

METHODS

Subjects

Sixty-seven marmoset (*Callithrix jacchus*) subjects were involved in this study: 38 females, and 29 males. These included juvenile, subadult and adult animals, ranging in age from six months to seven years old. Of these animals, 59 were subjects in the study, and nine were trained as demonstrators (one subject performed as a demonstrator after having been tested as a subject). The animals were drawn from the same population of animals described in the previous chapter, housed in a Medical Research Council facility. None had been subjected to any invasive research. All animals came from a total of 19 family groups and all testing was done within the family group, so that subject and demonstrator (or partner in group J – see Table 3 for details of conditions) came from the same home cage. Figure 1 in the previous chapter depicts the layout of the home cages.

Figure 6. – Schematic depiction of a marmoset opening the artificial fruit used in Study Two



Apparatus

A second “artificial fruit” was used which had been designed specifically for marmoset manipulation. The artificial fruit used in the current study was considerably simplified from the original design, such that it would be within marmoset manipulative capabilities. The dimensions of the apparatus were 12x6x6cm. The food reward could be accessed by reaching through a hole in the centre of one of the horizontal faces of the box. This hole was concealed behind a sliding door, which could be pushed either left or right. Figure 6 shows a schematic diagram of the artificial fruit used in this study, as operated by a marmoset. The food reward used was marshmallow (a highly preferred food), cut into approximately 0.5cm³ pieces.

Training of Demonstrators

Of the nine trained demonstrators, five were male and four were female. All were non-breeding group members. Training of the demonstrators was done in the home cage, with the animal isolated from the rest of the group members. Training sessions took place over three weeks, during which each demonstrator received up to five sessions. A method of shaping was used, initially allowing animals to remove food from the outside of the artificial fruit, then allowing them to remove food from inside the artificial fruit, but with the door open. Over subsequent sessions, the door was closed further until the demonstrator could access the food reward from the artificial fruit with the door fully closed.

Table 3. – Details of the testing sessions for the five groups of Study Two

Group	Experience phase	Trial
S (Condition 1) Scrounging (n=11)	Subjects could interact with a trained demonstrator. The artificial fruit was opened three times, with two pieces of food available each time.	
(Condition 2)	As O1 (below)	
O (Condition 1) Observation (n=12)	Subjects could observe a trained demonstrator from behind wire mesh. The artificial fruit was opened three times, with one piece of food available each time.	Subject was isolated with artificial fruit for five minutes.
(Condition 2)	As S1 (above)	
I Individual learning (n=12)	Subjects interacted alone with the (open) artificial fruit. A single piece of food was visible through the open door. Food was replaced to a maximum of three items.	
J Joint learning (n=12)	Subjects were paired and could interact with the (open) artificial fruit. Two pieces of food were visible through the open door. Food was replaced to a maximum of six items.	
C Control (n=12)	This group received no prior experience.	

Procedure

Subjects were assigned to five different experimental groups, as summarised in Table 3. Each testing session consisted of an experience phase (except for those individuals in the control group) followed by a trial. Individuals from groups I (individual learning), J (joint interaction with another naïve individual) and C (control group with no prior experience) only received one testing session each. However, as the effect of interaction and scrounging on learning, compared with pure observation, was of particular interest, groups S (scrounging) and O (observation) were given two sessions, counterbalancing the two types of experience. The experiment was designed in this way to allow investigation into whether those from the group that performed more poorly could achieve the same level of performance as the more successful group if provided with the (apparently) more effective type of experience. It was also necessary to be able to rule out the possibility that any difference in performance between the groups was simply due to individual differences (for example in motivation levels or neophobia). These two groups therefore gave rise to four conditions, S1 (joint interaction with a trained demonstrator, allowing scrounging), S2 (observation of a trained demonstrator through a wire mesh divider), O1 (observation, as S2) and O2 (scrounging, as S1).

All testing was done in the animals' home cage (see Fig. 1). Due to the way in which the home cage could be divided up (into four equally sized sections), sessions would commence when the required combination of individuals from the group had entered the top two sections. During experience phases involving pure observation of the trained demonstrator (conditions O1 and S2), demonstrator and subject were

separated by a wire mesh divider as shown in Fig. 1. During all other experience phases, the wire mesh divider shown in Fig. 1 was opened (although not removed altogether) such that the subjects (and demonstrator in scrounging conditions) could move freely around the top two sections of the enclosure.

The experience phase began when the artificial fruit was introduced. In sessions involving a trained demonstrator (S1, S2, O1 and O2) the artificial fruit was introduced closed and containing food, and was then opened a total of three times. The experimenter reloaded the artificial fruit in between openings by reaching into the cage, placing more food in the cavity, and sliding the door back to the closed position. During the other experience phases (for conditions I and J), the artificial fruit was introduced with the door open such that the food reward inside the cavity was visible. In these conditions the artificial fruit was reloaded up to two more times by replacing the food, although leaving the door in the open position. In each experience phase, the reward consisted of up to three food items per animal (a total of six items in the scrounging and joint learning conditions).

Each experience phase took five minutes (including reloading time), after which the demonstrator (or partner in condition J) was released into another section of the cage to rejoin the rest of the group (see Fig. 1). Trials followed immediately afterwards, during which subjects were isolated with the artificial fruit for 5 minutes. All testing was videotaped (both experience phase and test trials) for subsequent analysis.

Data Coding

For the experience phases, videotapes were coded in terms of whether or not the subject was interacting with the artificial fruit, and whether they took food from the artificial fruit. Interaction with the artificial fruit was defined as being within reaching distance of the apparatus, not necessarily touching it. Since the demonstration area was quite large (around 0.75m³ in volume), it was not at all difficult for the artificial fruit to be outwith the reach of the animal. The videotapes were used to identify the precise timings of onsets and conclusions of bouts of interaction with the artificial fruit. Test trials were coded in a similar way. Success in opening the artificial fruit was defined as the door opening fully (such that food could be removed), irrespective of method used. The judgement of success was never ambiguous, however, as in all cases when the door was opened, it was opened fully, and food was removed.

RESULTS

Behaviour of Groups During Experience

It was found that during the experience phase, subjects from group S did scrounge food. Only three out of the eleven subjects never took any of the food during the experience phase. Most of the demonstrations involved some degree of scrounging. During each experience phase, the artificial fruit was opened three times, resulting in a total of 33 demonstrations. In 45% of these, the demonstrator and subject each took one of the two food items; in 15% the subject took both pieces, and in 39% the demonstrator took both pieces.

Table 4. – Duration of contact (in seconds) with artificial fruit during experience phase, and the relationship between duration of contact and later success during the trial (values given for each of groups O2, S1, I and J, and all groups together)

Group	Duration of contact (mean and standard error)	Mean duration of contact		Succeeders vs. failers (Unrelated t-test)
		Succeeders	Failers	
Observation (Condition 2)	60.8 +/-13.7	67.4 (n=9)	41.0 (n=3)	<i>NS</i>
Scrounging (Condition1)	61.0 +/- 17.7	79.8 (n=8)	10.7 (n=3)	<i>P<0.05</i>
Individual Learning	63.2 +/- 11.2	96.5 (n=2)	56.5 (n=10)	<i>NS</i>
Joint Learning	47.2 +/- 8.88	59.7 (n=3)	43.0 (n=9)	<i>NS</i>
All groups (n=47)	58.0 +/- 6.38	73.5 (n=1)	44.2 (n=11)	<i>P<0.05</i>

Table 5. – Number of food items taken during experience phase, and the relationship between the number of food items taken and later success during the trial (values given for each of groups O2, S1, I and J, and all groups together)

Group	Number of food items taken (mean and standard error)	Mean number of food items taken		Succeeders vs. failers (Unrelated t-test)
		Succeeders	Failers	
Observation (Condition 2)	2.50 +/- 0.42	2.78 (n=9)	1.67 (n=3)	<i>NS</i>
Scrounging (Condition1)	2.27 +/- 0.56	3.12 (n=8)	0.00 (n=3)	<i>P<0.001</i>
Individual Learning	2.58 +/- 0.26	3.00 (n=2)	2.50 (n=10)	<i>NS</i>
Joint Learning	2.75 +/- 0.55	4.33 (n=3)	2.22 (n=9)	<i>NS</i>
All groups (n=47)	2.53 +/- 0.22	3.14 (n=1)	2.00 (n=11)	<i>P<0.01</i>

Groups I and J also received an experience phase during which they could interact with, and take food from, the artificial fruit, to allow investigation into the relative roles of individual learning and social support. As had been the intention, conditions I and J did result in levels of interaction with the artificial fruit during the experience phase that were equivalent to those of the scrounging individuals. Tables 4 and 5 show details of the amount of food items taken and the duration of contact with the artificial fruit during the experience phases for each of these groups. There was no difference between these groups either in terms of the amount of time they spent in contact with the apparatus during the experience phase (ANOVA: $F_{3,46} = 0.320$, *NS*) or the amount of food items taken (ANOVA: $F_{3,46} = 0.182$, *NS*).

Performance of Groups During Trials

The success rates of all of the groups are displayed in Table 6. There was an overall difference between the groups in terms of the success rate (Chi-Square test: $\chi^2 = 15.074$, $df = 4$, $P < 0.005$). Residuals (also displayed in Table 6) show that the only condition with an observed value significantly different from expected was group S, suggesting that the chi-square value is mainly accounted for in terms of the higher success rate of this group compared with the other four groups. This suggested that the scrounging group's experience was in some way more effective than the other groups', including those that had been provided with similar opportunities for individual learning and comparable levels of social support.

Table 6. - Success rates for all groups including standardised residuals (as calculated in accordance with Siegel & Castellan, 1988)

* indicates a result significant to $P < 0.005$

Group	Failure		Success		Total
	Number of individuals	Residual	Number of individuals	Residual	
Observation (Condition 1)	10	0.246	2	-0.663	12
Scrounging (Condition 1)	3	-1.024	8	2.752*	11
Individual Learning	10	0.246	2	-0.663	12
Joint Learning	9	0.049	3	-0.133	12
Control	11	0.443	1	-1.194	12
Total	43		16		59

Figure 7. – Number of individuals successfully accessing food from the artificial fruit following interaction with, versus pure observation of, a trained demonstrator

The order of presentation of these conditions was counterbalanced for two groups. Group O received purely observational experience first (O1) followed by scrounging experience (O2). Group S received scrounging experience first (S1) followed by purely observational experience (S2).

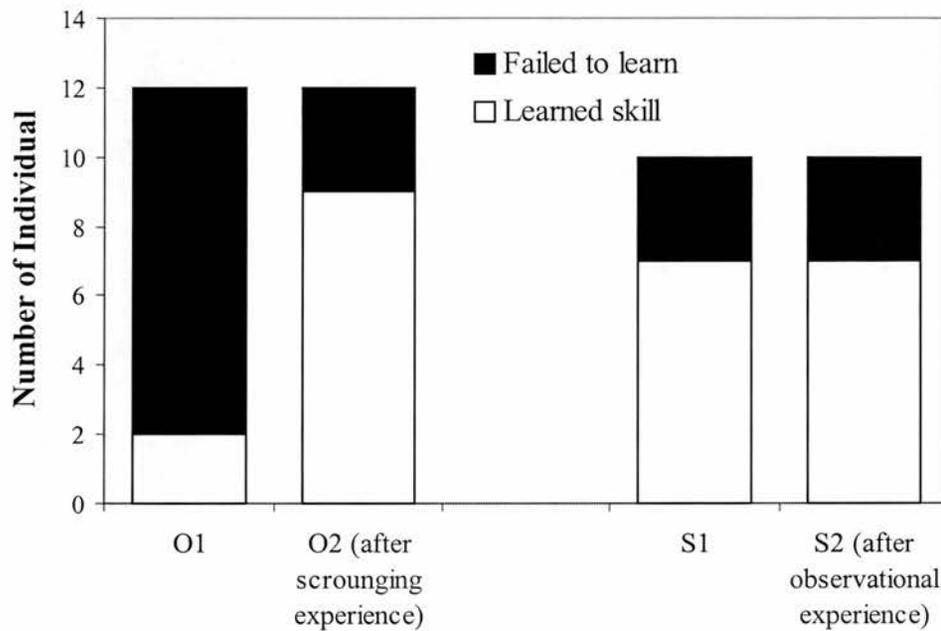
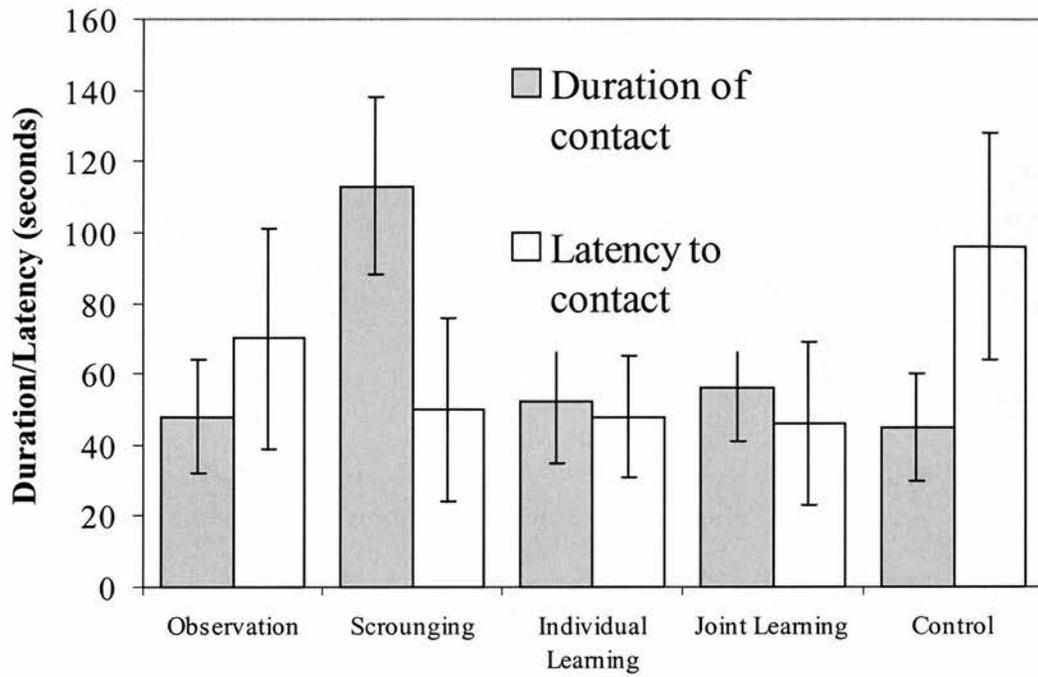


Figure 8. – Duration of contact (s) and latency to contact (s) with the apparatus during trials for the five groups (mean +/- standard error)



As the efficacy of scrounging experience relative to purely observational experience was of particular interest, these were directly compared. More individuals from the group that were allowed to interact with a skilled demonstrator (S1) successfully accessed food during the trial period, compared with those that had simply observed a skilled demonstrator from behind wire mesh (O1). The difference in success rate between these two groups was significant ($\chi^2_1 = 7.340$, Fisher's Exact Test $P < 0.02$, see Fig. 7 and Table 6).

It was clear that the difference between the two groups could not be attributed to individual differences. When group O were given subsequent scrounging experience, the success rate of this group improved significantly (Binomial test: $P < 0.01$) as illustrated in Fig 7. However, group S, when subsequently provided with the purely observational demonstration, showed no improvement (Binomial test: *NS*, also shown in Fig. 7). One subject was lost from group S prior to the commencement of the second condition as he was removed from his regular home cage for husbandry purposes. This subject was therefore omitted from this particular analysis.

Two other measures of performance on the trials were also looked at, duration of interaction with the artificial fruit, and latency to contact the artificial fruit (both shown in Fig. 8). As can be seen from the graphs, there was a trend for the Scrounging group to spend the largest amount of time in contact with the apparatus during the trial. However, the difference between the groups did not quite reach significance (ANOVA: $F_{4, 58} = 2.486$, $P = 0.054$). There was also a trend for the Control group to be slower than the other groups in their initial approach to the artificial fruit, but again the overall difference between the groups was not significant

(Kruskal-Wallis test: $H_4 = 6.804$, *NS*). Nonparametric statistics were used for analysis involving latencies to approach, due to the skewed distribution of this measure.

Predictors of Success

Judging by the differences between the groups, there was no apparent effect of the amount of experience on later success. However, when individual performance was analysed, success during the trial did appear to be related to behaviour during the experience phase. Tables 4 and 5 display differences in performance during the experience phase between individuals that succeeded on the subsequent trail, and those that failed. This has been done for the four conditions involving an experience phase during which the subject could interact with the apparatus (S1, O2, I and J), and all of those grouped together. As the tables show, for three of the individual conditions there were no significant differences in performance, either in terms of the amount of food taken, or the duration of contact with the apparatus. However, since in each case one of the groups being compared was extremely small (succeeders in groups I and J, and failers in group O2) this is not at all surprising. When the performance of each of the groups is combined, it can be seen that overall, succeeders both took more food (Unpaired t test: $t_{45} = 2.710$, $P < 0.01$) and spent longer in contact with the apparatus (Unpaired t test: $t_{45} = 2.404$, $P < 0.05$) during the experience phase. As can be seen from Tables 4 and 5, the only group to show significant differences on either of these measures was the Scrounging group. In this group the three subjects that did not open the artificial fruit during the trial had also spent very little time interacting with the apparatus during the experience phase and failed to take any food whatsoever. These three individuals may have been particularly timid, as there was no

apparent external reason for their hesitancy (such as aggression on the part of the demonstrator).

DISCUSSION

Why did Scrounging Facilitate Learning?

In the scrounging condition, in which subjects could closely interact with, and share rewards with, a trained demonstrator, social learning was strongly facilitated. This result cannot be attributed to individual differences between the groups as subsequent scrounging experience allowed another group to reach the same level of performance on the trials.

It also seems clear that this result cannot be explained simply in terms of individual learning of the object-reward association, or increased interaction with the apparatus due to social support. In the individual learning condition and joint learning condition, subjects were provided with equivalent opportunities to form the association between the artificial fruit and the food reward, as they were allowed to remove food items from the open artificial fruit. Furthermore, the group in the joint learning condition benefited from the social support of a partner during the experience phase, another factor which was suspected to have contributed to the success of the scrounging group. However, although they interacted with the artificial fruit during the experience phase, and removed food rewards from it, these two groups nonetheless failed to reach the level of success of the scrounging group when it came to opening the artificial fruit for themselves. In fact, both of these groups' success

rates were closer to the control group (that had received no pre-trial experience whatsoever) than to the scrounging group. Therefore, if the difference cannot be accounted for in terms of these two variables, there must be other factors involved which made the scrounging condition so conducive to learning, in comparison with the others.

Performance during the experience phase was clearly related to later success on the trial. However, the data suggest that this was principally due to individual differences (in levels of neophobia, for example), rather than the amount of learning about the apparatus. There were unambiguous differences between the groups in terms of success, despite their pre-trial behaviour being virtually identical in terms of amount of contact with the apparatus and amount of food rewards obtained. The most likely remaining conclusion is therefore that the scrounging group must have had access to some extra piece of information unavailable to the other groups.

The most plausible interpretation lies in the very close visual contact that was observed between subject and demonstrator in the scrounging condition, allowing the observer to learn more effectively the actions required. During the experience phase, the subject often came very close to the demonstrator and may have picked up more task-relevant information than those that observed through the wire mesh. This interpretation is also consistent with some of the other results reported. As was noted earlier, there was no significant difference between the five groups in latency to approach the artificial fruit (and as Fig. 8 shows, all except the control group behaved very similarly indeed), suggesting all were equally motivated to gain the food reward. The trend towards the scrounging group spending longer in contact with the apparatus

(also shown in Fig. 8) could potentially be interpreted as indicating higher levels of motivation in this group. However, the difference in manipulation time is probably more simply explained by the fact that succeeders (of which there were more in group S) were obtaining food, and therefore were less likely to cease their interactions with the apparatus. The only significant difference in performance between the groups was in the actual measure of trial success, suggesting that the scrounging group were the only group that were able to act effectively on this motivation.

Evaluation in Light of Previous Literature

This interpretation would also suggest some potential explanations for the contrast between the results presented here and those in the previous literature. In Giraldeau & Lefebvre's (1987) study, for example, no actual joint interaction occurred between demonstrators and scroungers. Pigeons in the scrounging condition were separated from demonstrators, the difference being that the food reward fell towards observers, as opposed to falling only into the demonstrator's cage. This could have led subjects to attend to the location of the food reward as opposed to the demonstration, whereas in the present study, subjects attended very closely to the demonstration in the scrounging condition.

In other studies, it may be the case that the dominance interactions of individuals may have hampered the potentially facilitatory effects of joint interaction. Nicol & Pope (1994) note, for example, that when they allowed observers to interact with demonstrators, often the demonstrator was threatened by dominant observers, inhibiting the demonstrator's approach to the apparatus. In some cases dominant

observers actually defended the apparatus, effectively preventing the demonstration. Thus, in the scrounging condition, fewer demonstrations were actually performed. No such effect was found in the study presented here, which is probably due to the generally tolerant nature of marmoset family groups.

When individuals are tested in groups, there will almost certainly be an economic interaction between producers and scroungers, such as that outlined by Barnard & Sibly (1981). However, this should not necessarily lead us to conclude that an individual that adopts the scrounger role has learned nothing from the experience. In Fragaszy & Visalberghi's (1989) study, for example, testing was done within the group, and therefore there would be little motivation for those individuals that had adopted a scrounging technique to switch to producing. A result from Lefebvre & Helder (1997) supports this suggestion. They note that, although none of the birds from one of their scrounging conditions ever produced in the group setting, all seven performed the opening technique when tested alone.

Lefebvre & Helder (1997) also report another result that suggests a further reason why group testing has tended to result in low levels of social learning. Pigeons that scrounged in a group learned a task less effectively than pigeons that had scrounged singly. They attribute their result to a confusion effect, involving attention being drawn away from the demonstrator to other individuals in the group. Therefore, in group studies of scrounging and social learning, it may not necessarily be the scrounging actions themselves that inhibit social learning, but the general distractions from the demonstration which are inherent to group testing.

Directed Social Learning

As noted in the introduction, there are apparent contradictions in the literature, with regard to whether or not information is liable to be transmitted via socially tolerant relationships. Coussi-Korbel & Fragaszy (1995) have referred to such identity-dependent effects as *directed* social learning. On the one hand, learners are more likely to pick up information from individuals with whom they interact closely, whilst on the other, this kind of joint interaction is liable to result in scrounging behaviour, which has generally been viewed as an inhibiting force in social transmission.

As noted by Fragaszy & Visalberghi (1989), social transmission of a suite of instrumental behaviours is generally assumed to occur in wild chimpanzees, and there is now considerable support for this view (e.g. Whiten et al., 2001). However, as pointed out by Fragaszy & Visalberghi (1989), the behaviours typically proposed to have been socially transmitted are those that are learned by infants while they are still with their mothers, a period in which the infant is free to interact with any of the same objects as the mother without any threat or punishment. Furthermore, they can do this at the same time as the mother demonstrates the behaviour (referred to by Fragaszy & Visalberghi (1989) as *coaction*). This type of joint interaction with a skilled individual (as opposed to observation followed by individual practice, for example) may be strongly beneficial to the learning of novel skills in non-human primates.

The marmosets in this experiment (all studied within their family group) showed the kind of tolerant interactions that we might expect to allow this kind of learning,

and therefore were an apt species in which to study the conditions under which scrounging facilitates social learning. The inhibitory effects of scrounging on social learning may have been overstated in the past, and scrounging, within the context of joint interaction with a skilled demonstrator and the relevant materials, may under some conditions facilitate social learning. Directed social learning may therefore be likely to be found in many other species, with information being transmitted preferentially via tolerant relationships.

Chapter Five

DEMONSTRATOR BEHAVIOUR IN OLIVE BABOONS AND COMMON MARMOSETS: SENSITIVITY TO OBSERVER CHARACTERISTICS

As was demonstrated in the previous chapter, close social interaction with a trained demonstrator did not inhibit social learning in common marmosets. In fact, success on the task in Study Two was significantly increased by opportunities to interact with and scrounge from the demonstrator.

It was proposed that this effect (which is in contrast to that described in much of the literature) may have occurred due to the more tolerant nature of marmoset family groups, compared with the social dynamics of species previously studied. One of the ways in which this could affect the outcome of social learning studies is in terms of the behaviour of the demonstrator. In previous studies of scrounging, group-testing conditions are sometimes reported to result in poorer demonstrations because observers may actively prevent the demonstration by hogging or defending the apparatus. Demonstrations may also be adversely affected in a more indirect manner, if the demonstrator is inhibited from performing in their presence. However, this effect may be less influential given a demonstrator-observer dyad with a tolerant relationship, such as the marmosets from Study Two.

It is now widely documented that there may be a dissociation between competence and performance under certain social conditions. Field reports from Van

Lawick-Goodall (1971) suggest that subordinate chimpanzees inhibited food-related problem solving activities when in close proximity to higher status individuals. Such phenomena have also been experimentally investigated in primates. Drea & Wallen (1999) proposed a “failure to perform” explanation for why only dominant individuals from a group of Rhesus monkeys appeared to learn a discrimination task. They tested this by training their group to separate into two cohorts, one composed of high-status families, and the other low-status families. Dominant individuals continued to perform to a high level under any social condition, but subordinates only performed well when separated from the rest of the group, within their low-status cohort. Malyukova & Molotova (1998) found that chimpanzees that had been individually conditioned to perform a discrimination task performed very differently when tested with another individual or in the group. In particular, the females of the group all performed very poorly (more passively, and with many fewer conditioned responses) in the presence of the male.

Such effects are not limited to primates. As mentioned in the previous chapter, Nicol & Pope (1994), studying domestic hens, note that demonstrations were impaired due to the presence of dominant observers that defended the apparatus and threatened the demonstrators. And Langen (1996), training Magpie-jays on a novel feeder task, found that three of his five trained demonstrators never performed the skill when in the presence of other, untrained jays.

Some authors have also suggested that skilled individuals may actively conceal information from potential exploiters. Menzel (1973) hid food in the presence of one chimpanzee, and found that this subject could quickly learn to modify her behaviour

such that they did not reveal the whereabouts of the reward to more dominant group members. More recently, Coussi-Korbel (1994) replicated Menzel's study with Mangabey monkeys, and found that the informed individual developed a number of tactics that helped him avoid losing his reward to the dominant male of the group. These included withholding information from the dominant male, and diverting his attention elsewhere before approaching the food.

Evidence of apparent concealment is also not limited to primates. Langen (1996) notes that the trained jays that failed to perform in the presence of conspecifics, "appeared to avoid attracting conspecifics: they did not vocalize, they scanned constantly, and they flew off at the approach of other members." (p163). Langen (1996) makes the tentative suggestion that, "perhaps trained jays were reluctant to demonstrate how to exploit a resource that others might utilize." (p165). Emery & Clayton (2001) have also found that food-caching scrub jays would re-cache a food item in a different location if it had originally been hidden in view of a conspecific (and hence potential thief). A similar effect has been described by Bugnyar & Kotrschal (2002) who found that ravens preferentially cache food when no other conspecifics are present.

All of this suggests that the performance of skilled individuals vary depending on the social context, and that this in turn could result in variability in the amount learned by observers. It seems clear from the studies reviewed that demonstrations are impaired particularly when there is a possibility of exploitation, or a certain amount of stress caused by the presence of the observer. This is liable to happen in particular when the observer is dominant to the demonstrator. Subordinate observers are

unlikely to be able to exploit the demonstrator so there is no reason for concealment. They are also much less likely to behave in an aggressive manner towards a demonstrator, so there would not be the same level of inhibition, or distraction from the task due to monitoring of the actions of the observer.

Dominance rank has already been proposed by several authors to be an influential factor in the likelihood that social learning will occur. As mentioned in the previous chapter, a review by Coussi-Korbel & Fragaszy (1995) discriminated two categories of social learning: “directed” and “non-specific” social learning (p1444). If a learner is more likely to adopt the behaviours of certain specific individuals within a population, then directed social learning is said to have occurred. If, however, the learner is equally likely to adopt the behaviours of any of the other individuals, the process is described as non-specific social learning. Coussi-Korbel & Fragaszy (1995) also proposed that amongst animals with hierarchical social structures, the social position of an individual was a particularly salient feature to conspecifics which could drive directed social learning.

To date, however, relatively little experimental research has been carried out to clarify in what manner dominance relationships might influence social learning. Strayer (1976) trained macaques (*Macaca nemestrina*) on an operant task in order to examine the effects of dominance on both individual and social learning. Dominant observers tended to make more responses overall, and the social learning condition resulted in them reducing the number of errors they produced. Subordinates, however, produced very few responses, although observing the trained individual allowed them to perform a greater number of rewarded responses. Observing the model therefore

allowed all subjects to produce higher *proportions* of rewarded responses versus errors. Nicol & Pope (1999) investigated the effect of demonstrator social status in domestic hens, *Gallus gallus*, using an operant pecking task. They found that the observer's operant pecking increased with both demonstrator social status and observer social status. Hens that observed cockerels, however, which are usually dominant to any hen, performed very few pecks.

If indeed demonstration quality can vary with observer identity, this could potentially provide another source of directed social learning driven by dominance rank. The first aim of the studies in this chapter was therefore to determine whether or not demonstration quality can be affected by the relative social rank of the observer.

A further goal was to determine whether variability in demonstrator behaviour could account in part for the apparent contrast between the results from Study Two and some of the previous research on the effect of scrounging on social learning. It may be the case that marmoset demonstrators are less adversely affected by the presence of an observer. Given that these animals are known to share food with other group members (Feistner & Price, 1991) avoidance of exploitation may be considerably less relevant. Furthermore, there is unlikely to be much stress associated with the close presence of a family member. In fact, Smith, McGreer-Whitworth, & French (1998) have documented that the presence of a pair-mate (in *Callithrix kuhli*, closely related to and with a similar social structure to *Callithrix jacchus*) actually reduces both behavioural and physiological stress responses to a novel situation.

Studies Three and Four therefore focus on different species; the common marmosets from Study Two, and another species in which it was predicted there would be much stronger effects of social context on the quality of the demonstrations.

Olive baboons were selected as a model species of the latter kind, as these animals are known to have a strongly linear hierarchical social structure (e.g. Castles & Whiten, 1998a, 1998b). Castles, Whiten, & Aureli (1999) have already shown differences in individual olive baboons' behaviour in the presence of dominant and subordinate individuals. The baboons showed much higher levels of stress-related behaviours in the proximity of dominant individuals. It was therefore likely that demonstrated behaviour might be similarly affected by the social rank of the observer.

In olive baboons it was predicted that trained demonstrators would inhibit their task-relevant responses in the presence of more dominant observers, compared with their behaviour in the presence of subordinates. It was also expected that this effect would be particularly pronounced in close social conditions when the animals could interact.

The behaviour of the marmoset demonstrators used in Study Two was also analysed. It was suggested in the previous chapter that scrounging did not inhibit social learning in marmosets partly because demonstrators were less adversely affected by the social conditions compared with some of the other species previously tested. If this is indeed the case then we would expect that observer rank-related effects on demonstrator behaviour would be much less pronounced than in the baboons.

For both of these species, the tasks selected for the demonstrations were ones for which it was known social learning facilitated acquisition. Marshall, Whiten, Caldwell, & Brent (1999) documented observational learning in olive baboons using an “artificial fruit” very similar to the original chimpanzee version (Whiten et al., 1996), but scaled down for manipulation by a large monkey. And the previous chapter shows a strong social learning effect in the marmosets. Both tasks had also been designed to be functionally analogous to real food-processing behaviour, involving manipulation to access an internal food reward (the edible “core”). It was hoped therefore that these tasks would be valid in terms of the type of skills likely to involve social transmission in these species.

It should be noted that whereas the marmosets were, again, tested within their family group, the baboons came from a large breeding colony in which the relatedness was unknown. As noted in Chapter One with regard to this (and the next) chapter, this undoubtedly influenced the outcome of the studies. However, since the group composition of either species was comparable to that found in the wild, it was considered that the results as collected were valuable in terms of discerning real influences on transmission. This issue will be returned to in the discussion of this chapter, and in the general discussion in Chapter Seven.

Study Three

DEMONSTRATOR BEHAVIOUR IN *PAPIO HAMADRYAS ANUBIS*

METHODS

Subjects

Sixteen male olive baboons, *Papio hamadryas anubis*, were studied. All subjects were juveniles, ranging in age from 2 to 5 years old. These subjects were drawn from a population of around 600 individuals free-ranging over a six-acre corral at the Southwest Foundation for Biomedical Research in San Antonio, Texas. For the purpose of running the experiment, the subjects were temporarily housed in a smaller group enclosure adjacent to the corral. Subjects entered the testing cubicles from this enclosure (Fig. 9). The subject group was split into two subgroups which were housed in this enclosure successively. Two of the sixteen animals (one from each of the subgroups) were assigned the role of demonstrator. Through food tests (see following section), five of the remaining subjects were classified as being dominant to their model, and nine subordinate. All animals were fed a diet of monkey chow and were supplied with water ad libitum.

Dominance Assessment

Dominance was tested between all dyads relevant to the study. An item of food was placed equidistant between two individuals in the group enclosure. An animal was judged to have prevailed if it took the food, and if this was not followed by any

kind of retribution on the part of the other member of the pair (e.g. chase, bite, threat face). If one member of the dyad consistently prevailed on this test (at least four times in a row) this individual was considered to be dominant to the other.

Apparatus

The testing cages used are shown in Fig. 9. They were separated from the group enclosure by guillotine doors which could be operated by the experimenter in order to let individuals into and out of the testing cages. The dimensions of the testing cages were 112cm(h) x 104cm (d) x 258cm (w). There were two transparent polycarbonate panels dividing the demonstration area and observation area. Again, these doors could be operated by the experimenter so individuals could either be separated, or could interact.

The task employed was again an “artificial fruit”. The version used in this study was designed for manipulation by large monkey species, and had previously been used by Custance et al. (1999) to test for imitation in capuchin monkeys (see Table 2b in Chapter Two), and as mentioned in the introduction also by Marshall et al. (1999) with olive baboons from the same population (although different individuals) used in this study. Figure 10 shows the artificial fruit used in this study, which was a box locked by bolts and a handle which must be removed to release a lid and gain access to the enclosed food reward.

Figure 9. – The baboon testing cages
Guillotine doors open into group enclosure. Sliding transparent polycarbonate doors (also operated by the experimenter) divide the observation and demonstration areas.

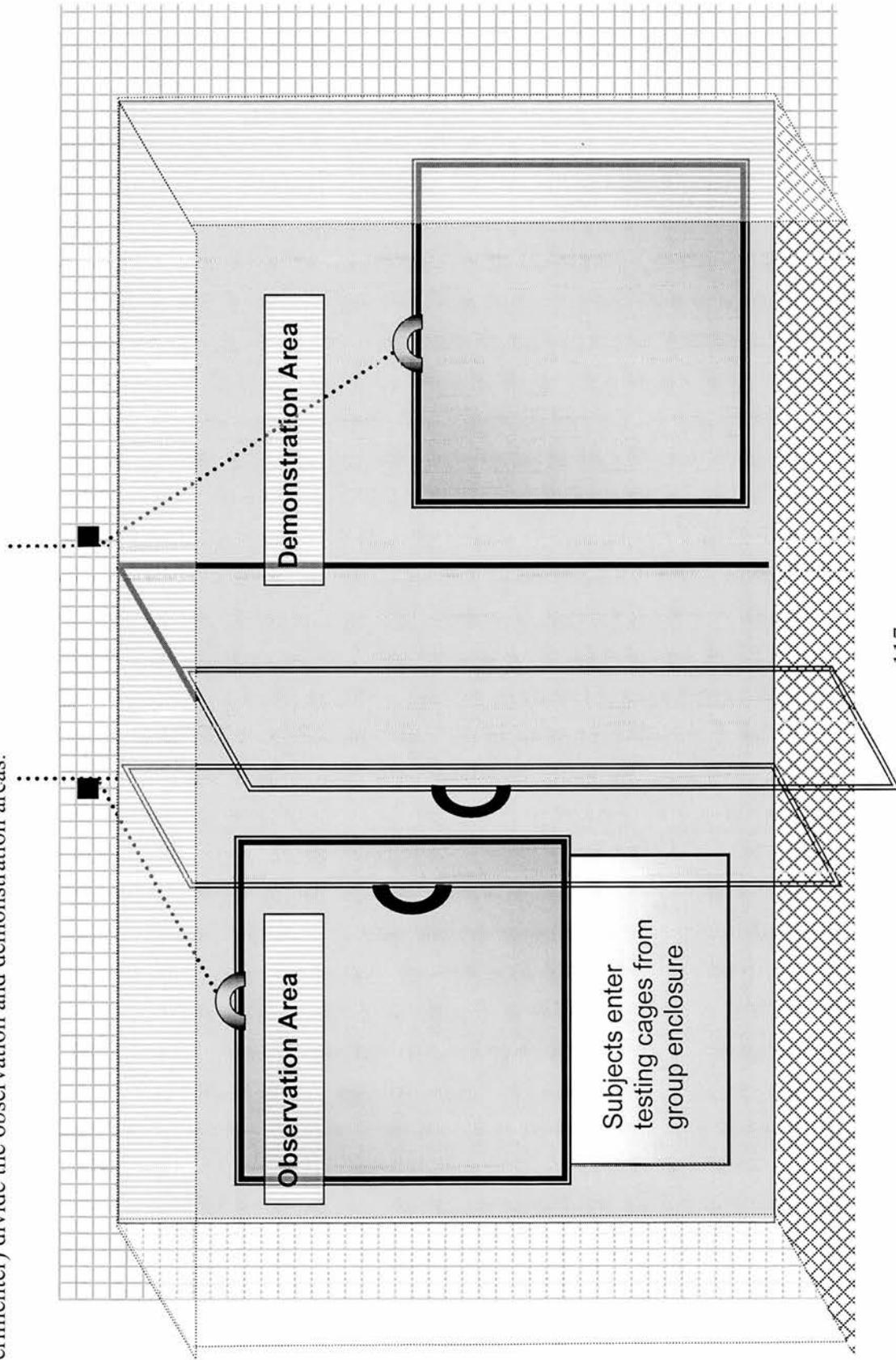
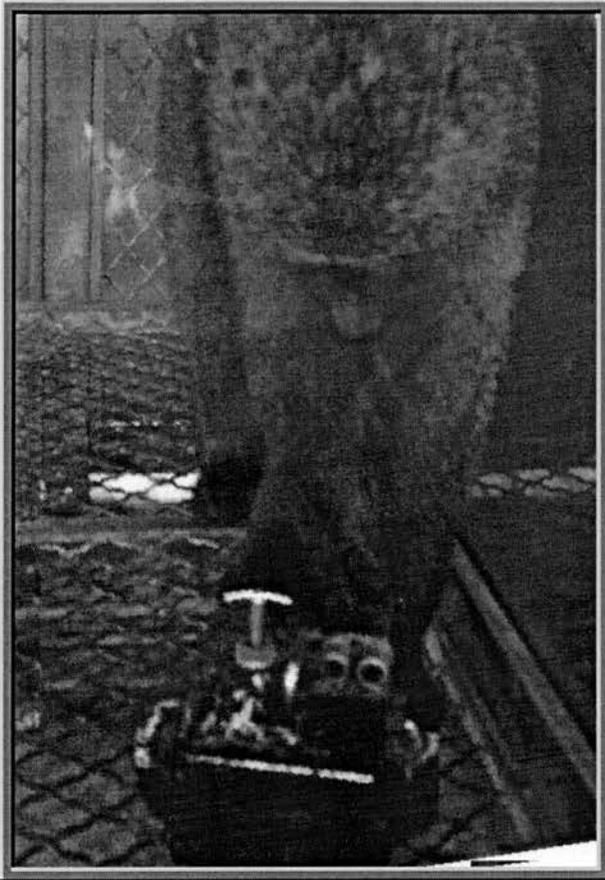


Figure 10. - A baboon operates the artificial fruit in the testing cages



Training and Habituation

The demonstrators were trained to open the artificial fruit using standard behavioural techniques (e.g. Pryor, 1985). Each of the demonstrators was trained over the course of a week (in the testing cubicles, isolated from the rest of the group), beginning with training the opening of the lid, and then gradually adding further defenses until the demonstrator could open the complete artificial fruit. Secondary reinforcement (a clicker) was used to pinpoint desired behaviours. Fruit was provided as the primary reinforcement, which was not a part of these baboons' regular diet (see subjects section) and was highly preferred.

The subjects were habituated to isolation in the testing cubicles in stages, first allowing them to enter and leave at will by keeping the guillotine doors open, and then providing food reinforcement for sitting in the cubicle with the door closed. By the time of testing, all subjects were entering the testing cubicles of their own accord.

Procedure

All subjects performed in two consecutive experimental conditions, these being i) Together and ii) Separated. In the Together condition, model and observer were in the testing cubicles (see Fig. 9), with the dividing doors open so that interaction was possible. In the Separated condition, the model was in the demonstration area and the observer was in the observation area, separated by the polycarbonate doors as shown in Fig. 9. To run trials, any subjects from the group were allowed to enter the testing cubicles from the group enclosure. When the required pair of individuals (model and observer) were in the cubicles the doors to the group enclosure were closed, and the

trial commenced. The trial was complete when the model had either demonstrated opening the artificial fruit three times, or after five minutes, whichever was first. The food reward was fruit as during training. Following this demonstration, the model was released from the demonstration area, and (in the Separated condition) the polycarbonate doors were opened to allow the observer to enter the demonstration area. Observers were allowed five minutes alone in the testing cubicles with the artificial fruit. All trials were videotaped for subsequent coding.

Data Coding

Videotape analysis was carried out in a similar manner to the previous two studies, in order to determine the number of demonstrations carried out in the time period, and the latencies to, and durations of the demonstrations.

Independent coding was also used in order to determine whether there was any evidence of active concealment on the part of the demonstrators. Coders were naïve to both the purpose of the study, and the identity of the baboons on the tape. Therefore if differences were found between the ratings given when observers were dominant compared with subordinate, then it could be assumed that there was a genuine difference in the demonstrators' behaviour. The coders were asked to answer five questions about each clip with a Likert scale rating. An example of the coding sheet used is given in Appendix II. Because the ratings were likely to be extremely subjective, two independent coders rated every clip, in order to provide a measure of inter-observer reliability.

RESULTS AND DISCUSSION

Rank-Related Effects

As the behaviour of two baboon demonstrators was investigated, the trials from each were treated separately, and meta-analytic procedures were employed to combine the results. In accordance with recommendations made by Rosenthal (1991), a number of methods of combining probabilities were employed to ensure that the overall p values calculated were relatively robust. In each case, three methods were used to combine the data, each returning similar overall p values. The methods selected (all described in Rosenthal, 1991) were: adding probabilities, adding logs, and adding Zs. Results reported here are those obtained using the method of adding Zs (Stouffer, Suchman, DeVinney, Star, & Williams, 1949, cited in Rosenthal, 1991).

It was found that there were differences between those demonstrations performed in the presence of dominant observers and those performed in the presence of subordinate observers.

In the Together condition, the demonstrators were less likely to perform the full three demonstrations when the observer was dominant, rather than subordinate, to themselves. For demonstrator 1, Chi-Square test: $\chi^2(1, N = 6) = 3$ Fisher's Exact Test *NS* ($Z = 0.84$), and for demonstrator 2, $\chi^2(1, N = 8) = 8$, Fisher's Exact Test $P < 0.05$ ($Z = 1.80$). Combining probabilities gave $Z = 1.87$, $P < 0.05$. Figure 11 displays the data for the number of instances in which demonstrators performed the full three demonstrations.

Figure 11. – Number of baboon demonstrators performing the full three demonstrations, and performing less than three demonstrations, when paired with dominant and subordinate observers, either separated from each other by a polycarbonate panel, or together, with the panel open

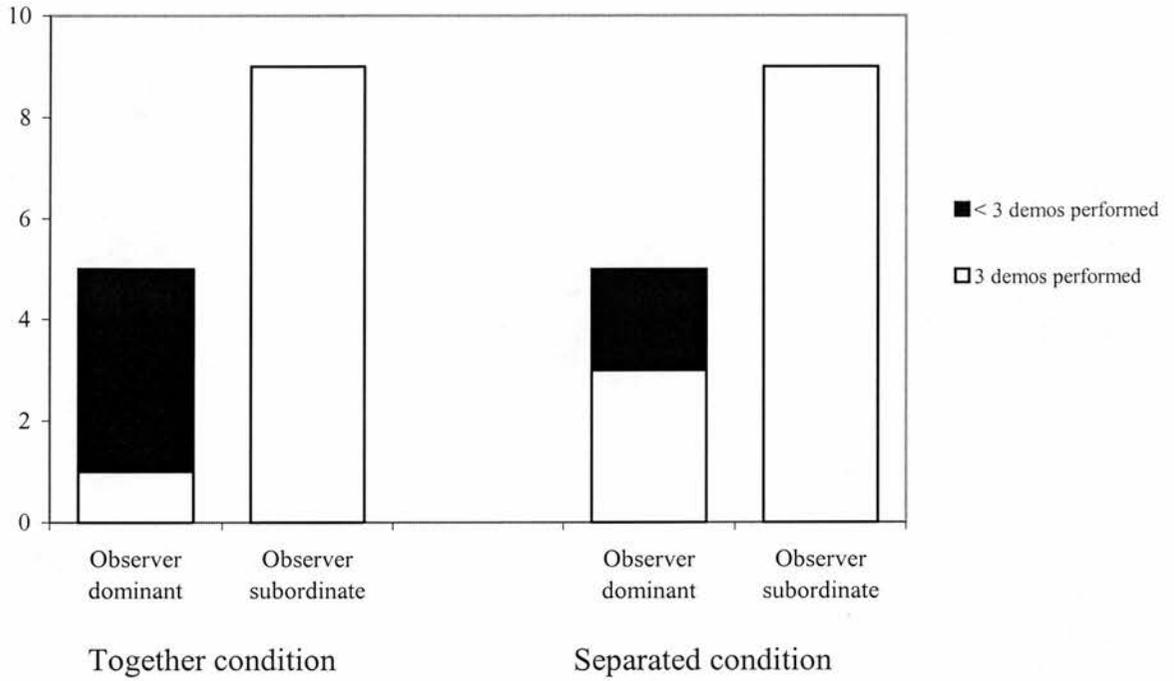


Figure 12. – Baboons: Latency to begin demonstrations when paired with dominant and subordinate observers, either separated from each other by a polycarbonate panel, or together, with the panel open

Results are shown separately for the two demonstrators in order to illustrate that the effect was similar for both individuals.

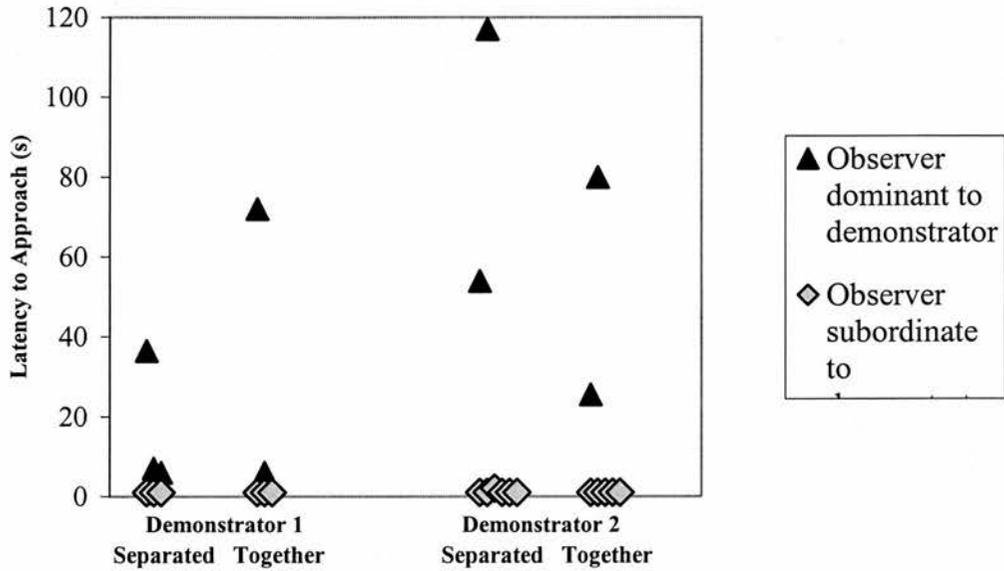


Figure 13. – Baboons: Duration of demonstrations (from approach to open) when paired with dominant and subordinate observers, either separated from each other by a polycarbonate panel, or together, with the panel open

Results are shown separately for the two demonstrators in order to illustrate that the effect was similar for both individuals.

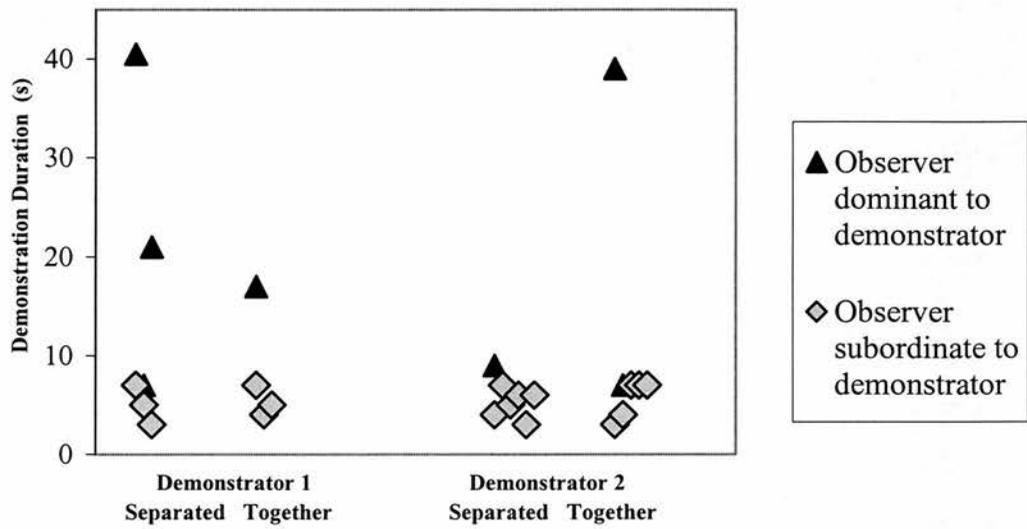


Figure 12 displays the data on the latency to begin demonstrations. When the observer was dominant, the demonstrators were slower to approach the apparatus. For demonstrator 1, Mann-Whitney U test: $U = 0$, $n_1 = 2$, $n_2 = 3$, $P < 0.05$, two-tailed ($Z = 1.94$). For demonstrator 2, $U = 0$, $n_1 = 2$, $n_2 = 6$, $P < 0.01$, two-tailed ($Z = 2.62$). Combining probabilities gave $Z = 3.22$, $P < 0.005$. Figure 13 displays the data on the duration of the demonstrations. In the Together condition there was a tendency for demonstrations to take longer from approach to completion when the observer was dominant. However, this difference was not significant for either demonstrator, or when combined. For demonstrator 1, $U = 0$, $n_1 = 1$, $n_2 = 3$, NS ($Z = 1.34$), and for demonstrator 2, $U = 4.5$, $n_1 = 2$, $n_2 = 6$, NS ($Z = 0.54$). Combining probabilities gave $Z = 1.33$, NS .

Independent coders' data provided some evidence of qualitative differences in the demonstrators' behaviour depending on the social status of the observer. Data on the reliability of the ratings is shown in Tables 7a and 7b. As can be seen from the table, the inter-coder reliabilities varied: some were very low, but others showed significant correlations across coders. However, all of those that were significantly correlated also showed significant differences between the ratings given when the observers were dominant, compared with subordinate, suggesting that where effects were clear they were evident to both coders alike. For the purpose of carrying out these inferential statistics on the data, the mean of the two coders' ratings was always used.

Table 7. – Independent coding data on behaviour during baboon demonstrations
 Table 7a displays data for the Together condition in which demonstrator and observer could interact, and Table 7b shows the results for the Separated condition, in which demonstrator and observer were divided by a polycarbonate panel.

Question number	Inter-rater reliability: Spearman's rho	Ratings		Difference between dominant and subordinate (Mann-Whitney <i>U</i>)
		Median +/- IQ range		
		Observer dominant to demonstrator	Observer subordinate to demonstrator	
Q1	0.316	3.5 +/- 3.0	2.0 +/- 0.8	<i>NS</i>
Q2	0.189	1.5 +/- 2.0	2.0 +/- 0.8	<i>NS</i>
Q3	0.488	4.0 +/- 4.25	1.0 +/- 1.5	<i>NS</i>
Q4	0.752**	5.0 +/- 2.75	2.0 +/- 2.5	<i>P</i> <0.05
Q5	0.400	4.0 +/- 4.0	2.0 +/- 2.5	<i>NS</i>

Question number	Inter-rater reliability: Spearman's rho	Ratings		Difference between dominant and subordinate (Mann-Whitney <i>U</i>)
		Median +/- IQ range		
		Observer dominant to demonstrator	Observer subordinate to demonstrator	
Q1	0.576*	4.0 +/- 3.0	1.5 +/- 1.5	<i>P</i> <0.05
Q2	0.314	2.5 +/- 2.0	1.5 +/- 2.0	<i>NS</i>
Q3	0.500	1.0 +/- 2.8	1.0 +/- 0.0	<i>NS</i>
Q4	0.542*	6.5 +/- 2.3	2.0 +/- 1.25	<i>P</i> <0.005
Q5	0.750**	6.0 +/- 2.8	1.5 +/- 0.8	<i>P</i> <0.005

Key:

- Q1 - How much attention did the observer appear to be paying to the demonstrator?
- Q2 - How much of the demonstration did the observer see?
- Q3 - To what extent did the behaviour of the observer actively prevent the demonstrator performing (e.g. hogging/defending apparatus, threatening behaviour)?
- Q4 - How closely did the demonstrator monitor the behaviour of the observer?
- Q5 - Did there seem to be a relationship between the attention of the observer and the timing of the demonstrations, i.e. did demonstrations appear to be performed selectively, when the observer's attention was elsewhere?

(See Appendix II for a copy of the rating scale given to independent coders)

* indicates a result significant to *P*<0.05

** indicates a result significant to *P*<0.01

In relation to discerning active concealment on the part of the demonstrator, the responses that are of most interest are those to questions 4 and 5. If the demonstrator was concealing their behaviour from the observer we would expect that they would time the demonstrations such that they were carried out when the observer's attention was elsewhere (Q5), and for this to happen, the demonstrator would need to be closely monitoring the behaviour of the observer (Q4). For the Together condition, the coders' responses to question 4, concerning the demonstrators' monitoring of the observer, were significantly correlated. Their responses also revealed a significant difference in the demonstrators' behaviour depending on whether the observer was dominant or subordinate. Demonstrators monitored the behaviour of dominant observers more than subordinate, as shown in Fig. 14. For demonstrator 1, Mann-Whitney U test: $U = 0$, $n_1 = 3$, $n_2 = 3$, $P < 0.05$, two-tailed ($Z = 1.99$), and for demonstrator 2, $U = 0$, $n_1 = 2$, $n_2 = 6$, $P < 0.05$, two-tailed ($Z = 2.01$). Combining probabilities gave $Z = 2.83$, $P < 0.01$.

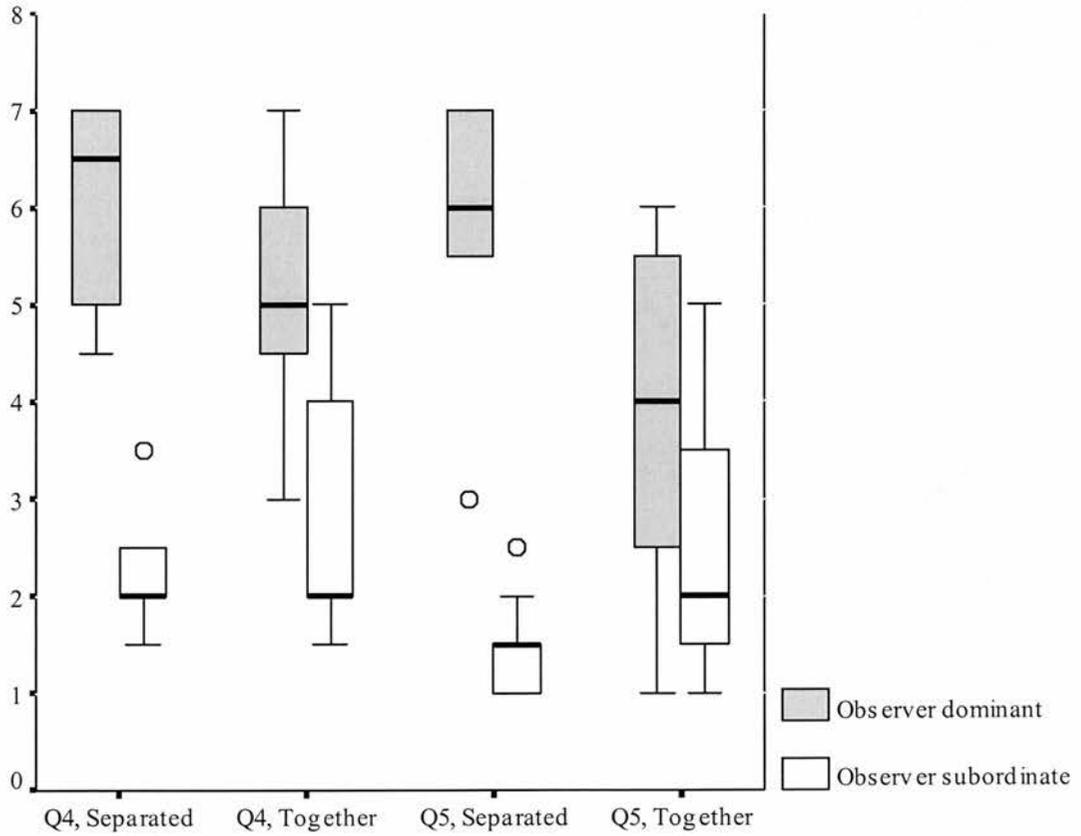
There was no significant difference between the coders' responses for dominant and subordinate observers on Q5, concerning the timing of the demonstration in relation to the observers' attention, also shown in Fig. 14. However, due to the very low correlation between the raters' responses on this question (see Table 7a), this is not surprising. It may well have been exceptionally hard to make this particular judgement in this condition. In the Together condition, therefore, the data provides no support for concealment from dominant observers, despite the difference in ratings to Q4. The demonstrators' greater monitoring of dominant observers may have simply been due to the fact that animals do tend to pay closer attention to more dominant individuals.

Figure 14. – Box and whisker plot of ratings given by independent coders on a Likert (1-7) scale to questions 4 and 5 for clips of baboon demonstrator behaviour under interactive (Together) and non-interactive (Separated) conditions, depending on the social rank of the observer relative to the demonstrator

Q4 – How closely did the demonstrator monitor the behaviour of the observer?

Q5 – Did there seem to be a relationship between the attention of the observer and the timing of the demonstrations, i.e. did demonstrations appear to be performed selectively, when the observer’s attention was elsewhere?

(See Appendix II for a copy of the rating scale given to independent coders)



Key:

- Median
- Box length Interquartile range
- Whisker Range, excluding...
- o Outliers, between 1.5 and 3 box lengths from the median
- * Extremes, over 3 box lengths from the median

For questions 1, 2 and 3 for the Together condition, there was no apparent difference in behaviour depending on the relative social rank of the observer. However, again due to the very low reliability scores (given in Table 7a), any significant differences would be highly unlikely.

In the Separated condition, there was a tendency for demonstrators to produce fewer demonstrations when the observer was dominant, rather than subordinate, to themselves (see Fig. 11). However, this result was not significant. For demonstrator 1, Chi-square test: $\chi^2 (1, N = 6) = 1.20$, Fisher's Exact Test *NS* ($Z = 0.00$), and for demonstrator 2, $\chi^2 (1, N = 8) = 3.43$, Fisher's Exact Test *NS* ($Z = 0.67$). Combining probabilities gave $Z = 0.474$, *NS*.

However, demonstrators did make a slower approach to the apparatus if the demonstrator was dominant (Fig. 12). For demonstrator 1, Mann-Whitney *U* test: $U = 0$, $n_1 = 3$, $n_2 = 3$, $P < 0.05$, two-tailed ($Z = 2.09$), and for demonstrator 2, $U = 0$, $n_1 = 2$, $n_2 = 6$, $P < 0.05$, two-tailed ($Z = 2.29$). Combining probabilities gave $Z = 3.10$, $P < 0.005$. Furthermore, these demonstrations were more hesitant, in terms of the time between initial approach to the apparatus and completion of the demonstration (Fig. 13). For demonstrator 1, $U = 0.5$, $n_1 = 3$, $n_2 = 3$, *NS* ($Z = 1.77$), and for demonstrator 2, $U = 0$, $n_1 = 2$, $n_2 = 6$, *NS* ($Z = 1.51$). Combining these probabilities gave $Z = 2.32$, $P < 0.05$.

Independent coding also provided some evidence for concealment in the Separated condition. Again, demonstrators appeared to monitor dominant observers more than subordinates (Q4) as shown in Fig. 6. For demonstrator 1, Mann-Whitney

U test: $U = 0$, $n_1 = 3$, $n_2 = 3$, $P < 0.05$, two-tailed ($Z = 2.13$), and for demonstrator 2, $U = 0$, $n_1 = 2$, $n_2 = 6$, $P < 0.05$, two-tailed ($Z = 2.02$). Combining probabilities gave $Z = 2.93$, $P < 0.01$. There was also evidence for concealment, with a clear difference between the ratings given to Q5 depending on the rank of the observer. When observers were dominant, demonstrators were more likely to time their demonstrations such that they performed them when the observer's attention was elsewhere (also shown in Fig. 14). For demonstrator 1, $U = 0$, $n_1 = 3$, $n_2 = 3$, $P < 0.05$, two-tailed ($Z = 2.05$), and for demonstrator 2, $U = 0$, $n_1 = 2$, $n_2 = 6$, $P < 0.05$, two-tailed ($Z = 2.02$). Combining probabilities gave $Z = 2.88$, $P < 0.01$.

Interestingly, the ratings given by the coders to question 1 for the Separated condition suggested that they believed that dominant observers were paying more attention to the demonstrations than subordinate observers ($U = 7.5$, $n_1 = 5$, $n_2 = 9$, $P < 0.05$, two-tailed). However, judging by responses to question 2, this apparently did not result in any advantage in terms of the amount of the demonstration that was seen ($U = 15.5$, $n_1 = 5$, $n_2 = 9$, *NS*) which may have been due to the concealing behaviour of the demonstrators. However reliabilities for this particular question are so low that there is little that can be concluded from this (see Table 1). Similarly, Q3 showed no significant difference between the ratings given for observers of different social ranks, but again the reliability measure for this question is very low (Table 1).

Effects of Social Interaction

It was proposed in the introduction that any rank-related effects on demonstrator behaviour found in the baboons would be particularly apparent in the Together condition, in which demonstrator and observer could interact. However, the present

data appears to provide little support for this view. As can be seen by looking at Figs. 12 and 13, these measures of latency to begin, and duration of, the demonstrations (providing an approximate measure of hesitancy and inhibition) showed very little difference between the Separated and Together conditions. No magnification of rank-related effects could therefore be found from this data.

Furthermore, the results from independent coders, regarding monitoring of the observer's behaviour, and concealment of their own skill, which can be seen in Fig. 14, in fact show *less* difference between the ratings given for subordinate and dominant demonstrators in the Together condition, compared with the Separated condition. In the case of question 4, this interaction was non-significant (ANOVA: $F_{1,12} = 1.791$, *NS*), but for question five there was a significant interaction between dominance rank and condition for the ratings given by independent coders (ANOVA: $F_{1,12} = 14.039$, $P < 0.05$). However, it should be noted at this point that this analysis is dependent upon the ratings given to Q5 in the Together condition, which as Table 7a shows, had a very low reliability coefficient. Therefore this effect may simply represent the contrast between a set of reliable ratings which show a clear effect (in the Separated condition), and a set of unreliable ratings which arose due to the difficulty of making a particular judgement (in the Together condition).

The results displayed in Fig. 11 merit note at this point. Although none of the measures picked up on any differences between the demonstrations given in the presence of dominant and subordinate observers, from Fig. 11 it can be seen that in fact fewer demonstrations were performed in the Together condition, with only one of the dominant demonstrators getting all three complete demonstrations. This may have

had the result of masking other effects. If demonstrators simply did not perform at all, it would make it much harder for independent coders to make the judgement required in question 5, to do with the timing of demonstrations. Furthermore, some data had to be excluded from the latency and duration analysis, as a demonstrator's failure to perform meant that these measures simply were not available in some cases. Therefore, in terms of judging concealment, hesitancy and inhibition, the most extreme cases of these (complete failure to perform) were not picked up on by the measures used. A summary of the measures used broken down by individual observer is given in Table 8, which illustrates this point.

It is therefore very difficult to draw any conclusions about the difference in baboon demonstrator performance between the Separated and Together conditions. However, it may be the case that under the interactive Together condition, the quality of information available to dominant observers *was* poorer, as the demonstrators' failure to perform is clearly even more likely to reduce social learning opportunities than qualitative differences in the demonstrations, such as variation in speed and timing.

Table 8. – Breakdown of demonstrator behaviour measures by individual observer (dominant observers only) for Together and Separated conditions

See Appendix II for greater detail of the questions answered by independent coders.

Dominant observer ID		13439	13510	13829	13526	13637
Demonstrator ID		14028	14028	14028	14129	14129
Together	Number of demos	0	3	0	1	1
	Median latency to begin (s)	72	6	N/A	25.5	80
	Median demo duration (s)	N/A	17	N/A	4	39
	Q4 – Monitoring	5	3	4.5	6	7
	Q5 – Concealing	5.5	2.5	1	4	6
Separated	Number of demos	1	3	3	3	0
	Median latency to begin (s)	36.5	7	6	54	117
	Median demo duration (s)	40.5	7	21	9	N/A
	Q4 – Monitoring	7	5	7	6.5	4.5
	Q5 – Concealing	7	5	7	6	2

In conclusion therefore, clear differences were found between the ways in which baboon demonstrators performed in the presence of dominant, compared with subordinate, observers. Much greater levels of hesitancy and inhibition of skills were found in the baboons' performances, and there was also evidence of the active concealment of the trained behaviours. It is clear therefore, that dominant observers were receiving poorer quality demonstrations, although very little can be concluded about differences between the interactive and non-interactive conditions. These issues will be discussed further later in this chapter, in the general discussion.

Study Four

DEMONSTRATOR BEHAVIOUR IN *CALLITHRIX JACCHUS*

METHODS

Subjects, apparatus and procedure were as described in Study Two in the previous chapter. However, on this occasion it was the nine demonstrators' behaviours that were of interest, rather than the observers'. Data coding was carried out in the same way as detailed in Study Three, including independent coding.

Dominance Assessment

As mentioned in previous chapters, the common marmoset extended family group is made up of an alpha male and female who are reproductively active, adult offspring whose reproduction is suppressed, and infant offspring. Individuals within the group are therefore generally best characterised in terms of one of these social

roles (Koenig & Rothe, 1991). The first set of analyses will therefore concern the behaviours of the demonstrators (all of whom were non-reproductive adult group members) with respect to observers of different role (parent vs. sibling).

However, there was a possibility that using social roles was not the most appropriate choice in terms of looking for sensitivity to observer identity. As described in Study Three, food tests were used to determine the relative dominance of the baboons, and this kind of dominance measure may have been more relevant to this study (involving food-finding behaviours). Therefore, the marmosets were also tested for dominance by using food tests in order to see if this provided any better a relationship between demonstrator behaviour and observer social rank. Each dyad relevant to the study was isolated, and a piece of food placed equidistant between them. As with the baboons, if an individual took the piece of food, it was judged to have prevailed. However, the behaviour of the marmosets was considerably more variable than the baboons so this was repeated ten times for each pair. If an individual gained the food at least seven out of these ten times, it was judged to be dominant to the other. Cases where neither individual was the clear winner were labelled as undetermined dominance. This gave three levels of social status for the observer: dominant to the demonstrator, subordinate to the demonstrator, and undetermined.

RESULTS AND DISCUSSION

Observer Social Role

The data for two of the demonstrators had to be discarded as it had only been possible to collect data for these individuals under a single observer condition (i.e. it would not have been possible to compare those individuals behaviour in response to dominant and non-dominant observers). The resulting marmoset data reported here was analysed in a different manner to the baboons. As there was a larger number of demonstrators (six), with a smaller number of trials per demonstrator (three or four per demonstrator), averages for each condition (dominant observer and non-dominant observer) were calculated for each individual, and then within-subjects analyses were carried out. However, the Stouffer method, although not reported here, was also carried out, (combining Mann-Whitney results for each individual demonstrator as had been done for the baboons) to rule out the possibility that the different methods of analysis were responsible for any apparent differences between the species. The use of this method did not alter the significance levels of any of the results.

In the Together condition, although the artificial fruit was always opened three times (as noted in Study Two in the previous chapter), on a small number of occasions the observer took over before the end of the demonstration period, so the demonstrators themselves did not always perform the full three demonstrations. Since this behaviour clearly represents a case of the observer actively preventing the demonstration by hogging the apparatus, this was analysed in order to find out if the likelihood of this happening was affected by social role in the marmosets. However,

as shown in Figure 15, this happened exactly as many times when the observer was a sibling, as when they were a parent (Chi-Square test: $\chi^2 = 0$, $df = 1$, *NS*).

The latency and duration of the demonstrations were also analysed, as they had been for the baboons. It was found that in the Together condition there was no difference in either the latency to begin (paired *t* test: $t_4 = 1.12$, *NS*), or the duration of the demonstrations ($t_4 = 0.31$, *NS*), according to the social role of the observer. These results are shown in Figs. 16 and 17, which display box and whisker plots of the combined data, as opposed to individual points as shown in the equivalent baboon figures (12 and 13), on account of the larger number of data points to be plotted.

Table 9 gives the inter-observer reliability measures for the ratings given by the independent coders. As can be seen, the reliabilities are extremely low (some actually negative), suggesting these judgements were virtually impossible to make in the case of the marmosets. Unfortunately, therefore, the data could not be used to carry out any inferential statistics.

In the Separated condition, there was much less variation in the number of demonstrations performed by demonstrators. All but one of the demonstrators performed the full three demonstrations (this trial had been excluded from Study Two in the previous chapter on the grounds that the observer had seen fewer demonstrations than other individuals in the same condition).

Figure 15. – Number of marmoset demonstrators performing the full three demonstrations, and performing less than three demonstrations, when paired with parents and non-reproductive group members (siblings), in the interactive Together condition

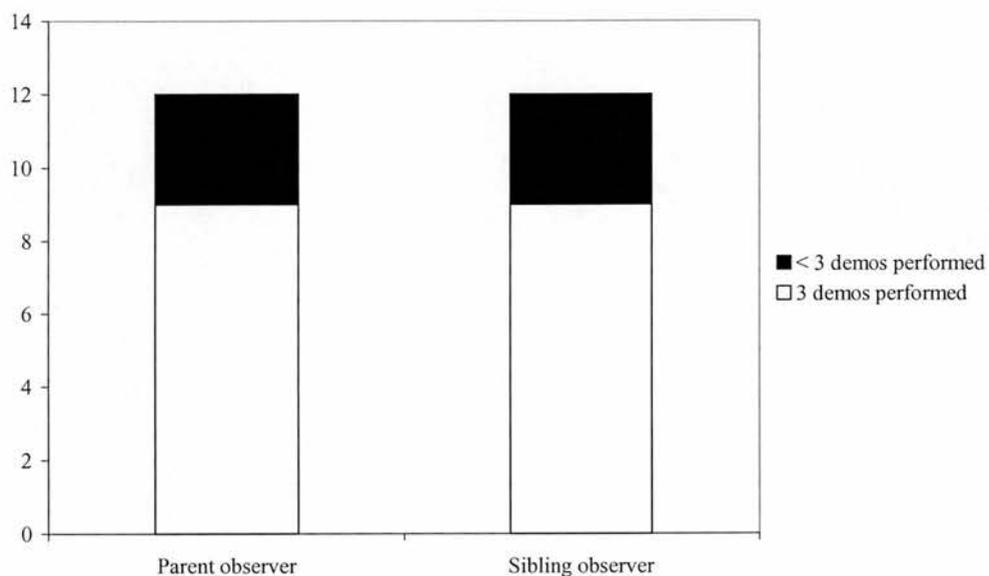
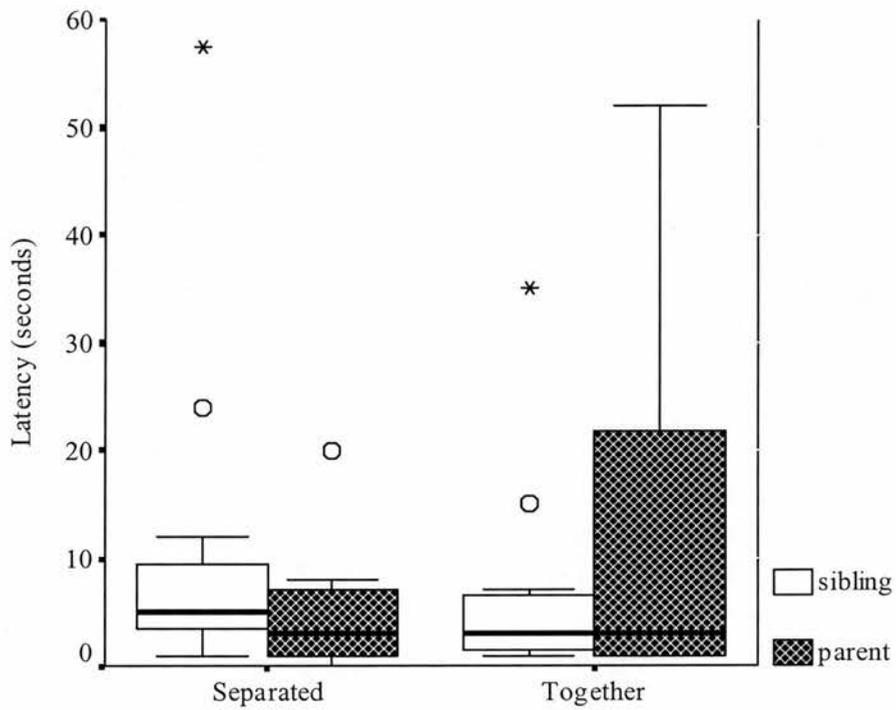


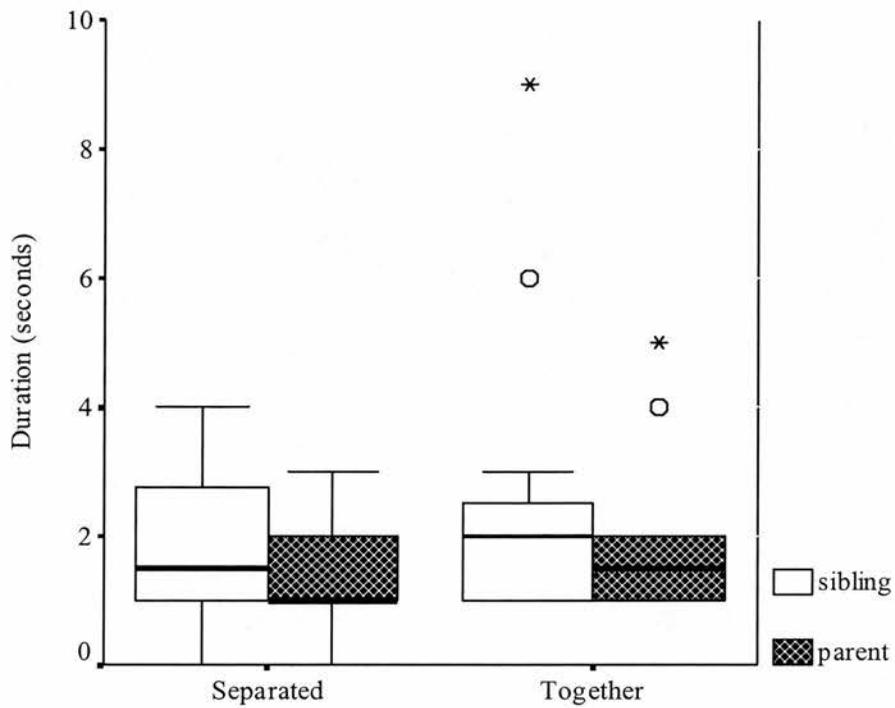
Figure 16. – Marmosets: Box and whisker plot of latency to begin demonstrations when paired with parent and sibling observers, either separated from each other by a wire mesh divider, or together, with the divider open



Key:

- Median
- Box length Interquartile range
- Whisker Range, excluding...
- o Outliers, between 1.5 and 3 box lengths from the median
- * Extremes, over 3 box lengths from the median

Figure 17. – Marmosets: Box and whisker plot of demonstration duration when paired with parent and sibling observers, either separated from each other by a wire mesh divider, or together, with the divider open



Key:

- Median
- Box length Interquartile range
- Whisker Range, excluding...
- o Outliers, between 1.5 and 3 box lengths from the median
- * Extremes, over 3 box lengths from the median

Table 9. – Inter-rater reliabilities (Spearman’s rho) for independent coding of marmoset demonstrator behaviour

See Appendix II for a copy of the rating scale given to independent coders.

	Together	Separated
Q1. How much attention did the observer appear to be paying to the demonstrator?	0.573**	0.268
Q2. How much of the demonstration did the observer see?	0.268	0.097
Q3. To what extent did the behaviour of the observer actively prevent the demonstrator performing...?	0.257	N/A†
Q4. How closely did the demonstrator monitor the behaviour of the observer?	0.443*	-0.120
Q5. Did there seem to be a relationship between the attention of the observer and the timing of the demonstrations...?	-0.356	-0.173

* indicates a result significant to $P < 0.05$.

**indicates a result significant to $P < 0.01$.

† There was not enough variability in the ratings given for this question to calculate a reliability coefficient.

There did not appear to be any effect of observer identity on the latency or duration of demonstrations in the Together condition either (displayed alongside the data from the Separated condition in Figs. 16 and 17). Whether a sibling or a parent was an observer made no significant difference to the demonstrator's latency to approach (paired t test: $t_5 = 0.98$, *NS*), or duration of the demonstration ($t_5 = 0.82$, *NS*).

Observer Dominance Using Food Test Measure

The food test measure appeared to be closely related to social role. Only one parent was judged through this measure to be subordinate to the demonstrator, whereas five siblings were. Furthermore, seven parents were judged to be dominant to the demonstrator, whereas no siblings were. Of those relationships that were classed as "undetermined", seven were siblings, and four were parents. The outcome of the food test was therefore significantly related to the social role of the observer (Chi-Square test: $\chi^2 = 10.5$, $df = 2$, $P < 0.005$).

However, this measure provided no better a relationship with demonstrator behaviour. Trials were again divided into "dominant" conditions (observer dominant to demonstrator) and "non-dominant" (including both subordinate and undetermined). This classification meant that two further demonstrators' data had to be excluded as none of their observers were classified as dominant. Once this had been carried out however, the remaining trials showed a perfect match with the social role method in terms of their classification into dominant and non-dominant. Latency to begin the demonstration showed no significant relationship with observer dominance (paired t test: $t_3 = 1.16$, *NS*, for the Together condition, and $t_3 = 0.40$, *NS*, for the Separated

condition). Similarly, the results for demonstration duration showed no effect of observer identity ($t_3 = 0.30$, *NS*, for the Together condition, and $t_3 = 1.46$, *NS*, for the Separated condition).

Effects of Social Interaction

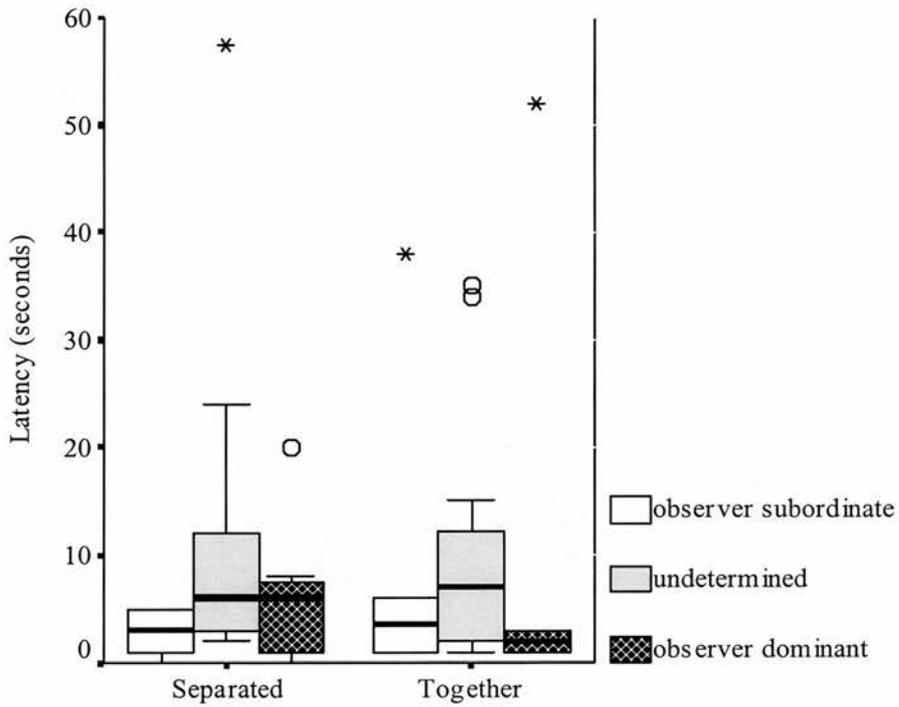
For the marmosets (as had also been the case with the baboons) it is apparent from the graphs (Figs. 16 and 17 in this case) that the Separated/Together manipulation had no effect on demonstrator behaviour in the marmosets. However, this finding is clearly worthy of note within the context of the results of Study Two in the previous chapter. The coding carried out in this chapter shows that there was very little variation in the behaviour of the demonstrators between these two conditions, which is consistent with the interpretation that social context had not adversely affected demonstrations in any way.

General Discussion

Sensitivity to Observer Social Status

As predicted, there were strong effects of the social rank of the observer on the behaviour of baboon demonstrators. No such effects could be detected in the behaviour of marmoset demonstrators. It must be concluded that marmosets are either not affected by the identity of observers, or more likely, that these effects are considerably less pronounced in this species than in the baboons.

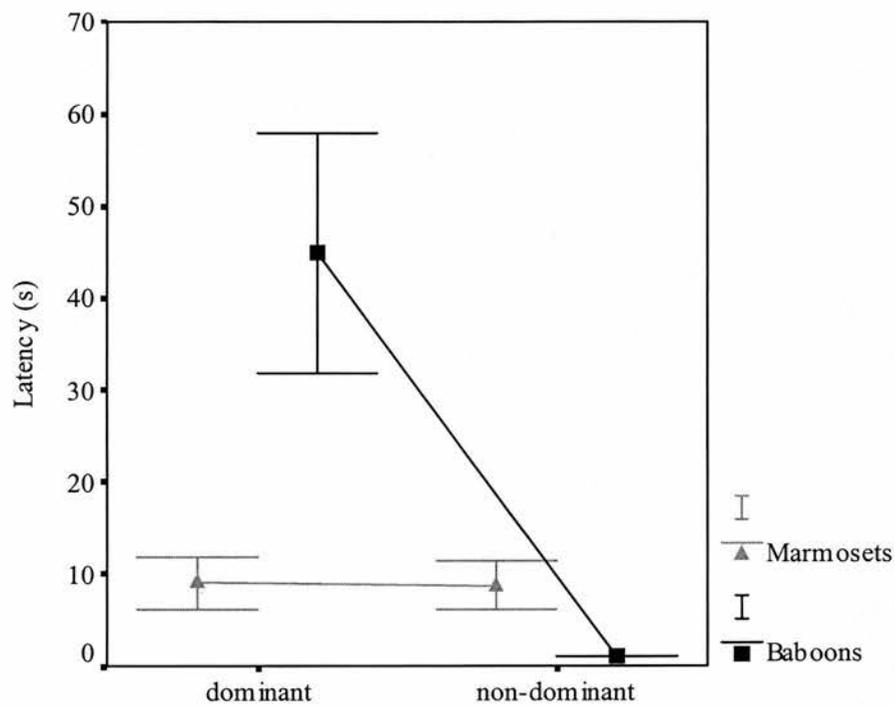
Figure 18. - Marmosets: Box and whisker plot of latency to begin demonstrations when paired with observers of different social rank (as determined by food tests), either separated from each other by a wire mesh divider, or together, with the divider open.



Key:

- Median
- Box length Interquartile range
- Whisker Range, excluding...
- o Outliers, between 1.5 and 3 box lengths from the median
- * Extremes, over 3 box lengths from the median

Figure 19. – Latency to begin demonstrations for marmoset and baboon demonstrators, in the presence of dominant and non-dominant observers (mean +/- standard error)



These results therefore provide some support for hypotheses put forward by Coussi-Korbel & Fragaszy (1995), who not only proposed social rank as a source of directed social learning, but also suggested that directed social learning might be less common in species with tolerant egalitarian social structures, compared with those that live in despotic societies. As shown in this chapter, sensitivity to observer identity can have a powerful effect on the quality of demonstrations, and therefore could potentially drive directed social learning. If certain species show less sensitivity to observer identity, then directed social learning might be considerably less likely in these species.

The species chosen for study do indeed have very different social structures, that can be characterised as despotic (the olive baboons) versus co-operative (the common marmosets). It would be premature to make generalisations about how every species with these types of social structure might behave under the conditions described in this chapter, but the differences are certainly striking, as illustrated in Figure 19. Currently, it can be concluded that social structure *may* affect patterns of social learning through variability in demonstrator behaviour under different social conditions, but this is as yet a very tentative conclusion. However, if similar patterns are found in other species with social structures that contrast in these ways, especially in the case of comparison groups that are phylogenetically very close, and with otherwise similar ecology, then the results could much more readily be generalised. These issues will be returned to in the General Discussion in Chapter Seven.

Effects of Social Interaction

It was also predicted in the introduction that any sensitivity to observer identity would be particularly significant in the interactive Together condition, and that demonstration quality would therefore be reduced in this condition. However, no conclusive support could be found for this hypothesis. This contrasts with results reported by Nicol & Pope (1994) in hens, discussed in the previous chapter. It may be the case that demonstration quality *was* affected in the baboons, but that this could not be detected within the current data set. There were very few dominant observers, and results for the subordinate observers in all cases showed floor effects. It may also be the case that dominant baboons are sufficiently intimidating to demonstrators that whether or not they were actually physically separated made little difference.

Implications for the Interpretation of Study Two

Nonetheless, the data do throw some light on the results of Study Two in the previous chapter. As mentioned previously, certain social contexts are liable to impair demonstrations (close interactive conditions may be necessary for this to happen in hens, although in this chapter it appeared that the mere presence of a dominant individual was sufficient to affect a baboon demonstration). However, the marmosets' demonstrations appeared unaffected by either the identity or proximity of the observer. Marmoset demonstrators were clearly not inhibited by the social conditions of the study, which may go some way towards explaining why a facilitatory effect of scrounging was found in the previous chapter. It may therefore be the case that if other species are studied which perform in a similar way to the marmoset

demonstrators in Study Four then those species may also show a facilitatory effect of close social interaction on social learning.

Interpretation in Light of Previous Literature

The current results contribute to an understanding of the ways in which dominance rank can influence social learning. As described by Nicol & Pope (1999), certain individuals may be more effective demonstrators irrespective of differences in performance. Their hen observers responded most effectively after having observed dominant as opposed to subordinate demonstrators. Nicol & Pope (1999) suggest this could be either a selective bias on the basis of the prior foraging success of dominant individuals, or simply because observers attend more closely to aggressive individuals. However, in studies where differences in demonstrator performance are found, such as those described in this chapter, this may also result in significant influences on transmission patterns, as the quality of the demonstrations may be strongly influenced by the relative rank of the observer.

It is also clear from this chapter, however, that rank-dependent effects on demonstration quality are not universal. Drea & Wallen (1999), in their study of rhesus monkeys learning in social groups, suggest that subordinate animals “play dumb” in high-status company, and liken it to humans allowing their boss to win at a competitive sport. However, this interpretation may be flawed, as it suggests that both human and monkey are constrained in their performance *by their role*. Although this may be true of humans, subordinate rhesus may be merely avoiding aggressive competition over a food reward (a prize which they are almost certain to lose to a

more powerful individual in any case). Such “playing dumb” behaviour in animals may disappear as soon as this is no longer a concern. In marmosets, the alpha male and alpha female are clearly the heads of the group, yet subordinate individuals in this study did not appear to inhibit their food-finding skills in their presence.

Directed Social Learning

In terms of the implications for directed social learning, therefore, it seems that, as Coussi-Korbel & Fragaszy (1995) suggested, directed social learning may be less likely in groups with more tolerant, egalitarian social structures. However, it is worth noting at this point that all marmosets were tested within their family group.

Marmoset demonstrators might have behaved very differently indeed in the presence of a non-group member, as marmosets are a territorial species and are typically aggressive to members of other groups. The reason that this was *not* tried was that it was considered potentially very stressful for the individuals involved. Therefore, although information may spread evenly within a family group this should not be taken to imply that information will spread evenly throughout an entire population.

A further conclusion from this chapter might seem to be that, in terms of patterns of directed social learning, in despotic populations at least, transmission from subordinate to dominant may be considerably less likely than transmission in the opposite direction. However, there are other ways in which dominance status might influence who learns from whom. There may also be constraints on transmission from dominant to subordinate, if low-ranking animals are inhibited from approaching

dominant demonstrators and the objects with which they interact. This issue will be examined in the following chapter.

Chapter Six

CONSTRAINTS ON LEARNING FROM A DOMINANT DEMONSTRATOR

The previous chapter provided some support for the suggestion that there may be obstacles to skill transmission from subordinate to dominant individuals within hierarchical groups. However, some authors have also proposed that in addition to this, there may also be barriers to transmission in the opposite direction, from dominant to subordinate. Visalberghi & Fragaszy (1990) point out that individuals of low social status will be constrained by social factors to limited access to desirable objects, and therefore will be afforded fewer opportunities to refine any motor skills involved in manipulating those objects. Furthermore they propose that (as discussed in Chapter Four) coaction of a skilled model and a learner may be the most effective setting for learning of a novel motor skill in nonhumans. Visalberghi & Fragaszy (1990) suggest that this phenomenon is, “probably restricted almost exclusively in normal circumstances to mother-infant pairs” (p267). Clearly there will be some exceptions to this general rule, but it is certainly improbable that a skilled dominant individual manipulating a valued object would tolerate the close presence of a more subordinate animal.

As shown in Study Two in Chapter Four, joint interaction with a skilled demonstrator *did* produce effective conditions for learning. This therefore supports the suggestion that joint interaction can have a powerful influence on transmission, and that it is more effective than for example, accessing the same object *after*

observing the demonstrator (as might be likely for a subordinate learner). As Study Two showed, those subjects that interacted with the apparatus following pure observation of a skilled demonstrator were little more successful than those that saw no demonstration at all.

The aim of the current chapter was therefore to identify whether subordinate animals were prepared to interact jointly with a dominant individual, and whether the presence of the dominant individual in fact masked any social learning effect due to the inhibition of the observer. In order to investigate this, olive baboons were again selected as a model hierarchical primate species. However, once again, it was expected that the behaviour patterns shown by a less hierarchical and more cooperative species would be considerably different. Common marmosets were therefore also studied again, for the purpose of comparing their performance with that of the baboons, under comparable social circumstances.

The two studies described here (Study Five with olive baboons, and Study Six with common marmosets) each involved three main conditions (as shown in Table 10). Subjects from the control groups saw no model, whereas those from the other groups saw a dominant model interacting with a novel object, and were then either given the opportunity either to join this dominant individual, or, following removal of the dominant model, to interact with the novel object alone. It was anticipated that this would allow a measure of how much subjects were facilitated towards the object by having observed a model, by looking at the differences in behaviour between the Model Removed group and the No Model group. In addition to this, the difference between the Model Present and Model Removed group could provide a measure of

how much the continued presence of the dominant model either inhibited (as predicted in the case of the baboons) or facilitated (as might be expected in the case of the marmosets) behaviour towards the novel object.

Study Five

THE SOCIAL INFLUENCE OF A DOMINANT MODEL IN *PAPIO HAMADRYAS ANUBIS*

METHODS

Subjects

The subjects were drawn from the same two groups of olive baboons described in the previous chapter, housed at the Southwest Foundation for Biomedical Research in San Antonio, Texas. Twenty-six of these animals were involved in this study, of which 19 were male and 7 were female. All subjects were juveniles, ranging in age from 2 to 5 years old. Two four year-old male subjects were shaped to act as models, and the remaining 24 animals were assigned the role of observer. In each case, the animal given the role of model was the most dominant male of his group (see previous chapter for details of the two subgroups, and of dominance testing). All animals were fed a diet of monkey chow and were supplied with water ad libitum.

Table 10. – Summary of the conditions of Studies Five and Six

Study Five, with baboon subjects, involved only three conditions (n=8 in each): Model Present, Model Removed and No Model. Study Six, with marmoset subjects, incorporated two more conditions involving extra models: the five conditions (n=6 in each) were therefore One Model Present, Two Models Present, One Model Removed, Two Models Removed and No Model.

	Observation Phase	Testing Phase
Model(s) Present	The subject was in the observation area, and the model(s) were feeding from the novel object in the demonstration area.	The dividing partition was opened to allow the subject to join model(s) in demonstration area
Model(s) Removed	As Model Present (above)	The model(s) were allowed to leave the demonstration area. The dividing partition was then opened to allow the subject to enter the demonstration area.
No Model	The subject was in the observation area, and the novel object was in the demonstration area.	The dividing partition was opened to allow the subject to enter demonstration area.

Apparatus

The testing cubicles used were the same as those used in Study Three in the previous chapter, and shown in Fig. 9. An open plastic box-shaped container (8 x 10 x 12 cm) containing strawberry jam (a highly preferred food and, as in the previous study, not part of their usual diet) was used as the novel feeder.

Training and habituation

The subjects were habituated to isolation in the testing cubicles as described in the previous chapter. The two models were habituated to the novel feeder by exposing them to it (in isolation in the testing cubicles) on several occasions, until they were reliably feeding from it. Models were also trained to enter the testing cubicles on command.

Procedure

Subjects were randomly allocated to one of the three conditions: Model Present, Model Removed, and No Model (see Table 10). The apparatus was introduced to the demonstration area before either individual entered the testing cubicle. An observer was then allowed to enter the observation area. The model (Model Present and Model Removed conditions) would then enter the demonstration area on command. All trials consisted of an observation phase and a testing phase. During the observation phase, model and observer were separated by the transparent polycarbonate dividers in the testing cubicles, as shown in Fig. 9 (the observer was simply separated from the novel feeder in the No Model condition). Each observation phase lasted between 60 and 120

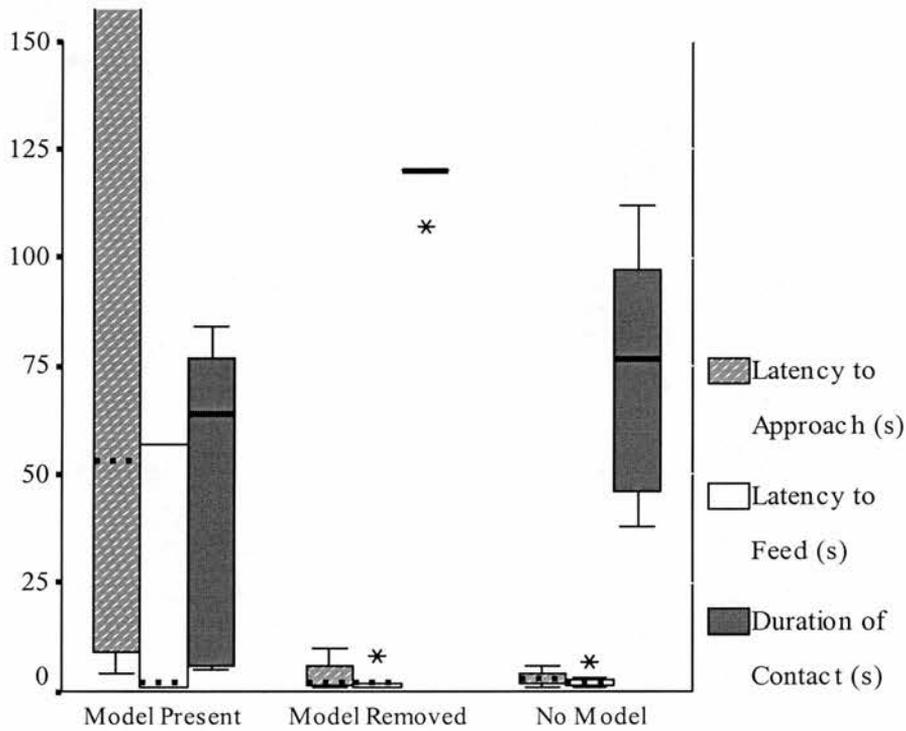
seconds. Following the observation phase, in the Model Removed condition the model was allowed to exit the testing cubicles via the guillotine door in the demonstration area which opened into the group enclosure. The polycarbonate divider was then opened so that the observer was free to enter the demonstration area. In both No Model and Model Present conditions, the polycarbonate divider was simply opened immediately after the observation phase. Each testing phase lasted at least 120 seconds, and was timed out after 180 seconds if the subject had failed to approach the apparatus during that time. All trials were videotaped for subsequent coding.

Data Coding

Videotapes of the testing phases were coded in terms of the observers' behaviour towards the apparatus. A cut-off point of 120s from the first approach was chosen as this kept the time period constant for each subject, and prevented any differences between subjects occurring simply due to the remaining quantity of food. Each interaction of a subject with the novel object was coded. Interaction was defined as it had been in Study Two, as coming within reach of the apparatus. Approach was therefore the first point at which this occurred. As the testing cages were quite spacious (approx. 3m² in volume) it was not difficult for the apparatus to be outwith the reach of the animal. Measurements of particular interest were i) latency to approach apparatus from time of door release, ii) latency to begin feeding from time of approach, and iii) total duration of contact with apparatus during the 120s following approach. Three subjects failed to approach the apparatus within the trial period, so their data were excluded from the second two measures.

Figure 20. – Behaviour towards a novel object for baboon subjects from the three groups:

Model Present (in which a dominant model was present before and during the test period); Model Removed (in which a dominant model had been observed, but was released before the test period); and No Model (in which no model was observed at any time)



Key:

- Median
- Box length Interquartile range
- Whisker Range, excluding...
- o Outliers, between 1.5 and 3 box lengths from the median
- * Extremes, over 3 box lengths from the median

RESULTS AND DISCUSSION

Figure 20 displays the data on all of these three measures for the three groups of baboon subjects. Latency of approach showed a significant difference between the conditions (Kruskal-Wallis test: $H_2=13.081$, $P<0.001$), as did the duration of interaction with the novel object (Kruskal-Wallis test: $H_2=14.471$, $P<0.001$). Latency to begin feeding after approach showed no difference between the groups however (Kruskal-Wallis test: $H_2=0.541$, *NS*).

Post-hoc comparisons between groups were carried out in accordance with Siegel & Castellan's (1988) recommendations for multiple comparisons between groups. It appeared that having seen a model did to some extent heighten subjects' interest in the novel object, as post-hoc comparisons between the Model Removed and No Model conditions showed that those in the Model Removed condition spent longer interacting with the novel object ($P<0.05$). Seven out of the eight subjects from this group in fact performed at ceiling level, spending the entire duration of the coded time period in contact with the apparatus, as can be seen from Fig. 20. Thus, there was a general stimulus enhancement effect. However, the Model Removed group were not significantly quicker to approach the novel object than the No Model group.

The continued presence of the dominant model clearly masked these social effects however. Not only were the subjects from the Model Present condition slower to approach the apparatus than those from the Model Removed condition ($P<0.05$), they were also significantly slower than those from the No Model condition ($P<0.05$).

Furthermore, the three subjects that failed to approach the apparatus during the allotted time period were all from the Model Present condition. This meant that the presence of the dominant model during testing made approach significantly less likely ($\chi^2_1 = 6.857$, Fisher's Exact Test: $P < 0.05$). The Model Present group also spent less time interacting with the novel object than those from the Model Removed group ($P < 0.05$), although they were not significantly slower than the No Model group.

The results therefore provide support for the general hypothesis that in baboons the continued presence of a more dominant model may not only mask social learning effects but may also inhibit opportunities for learning compared to an entirely non-social situation.

Study Six

THE SOCIAL INFLUENCE OF A DOMINANT MODEL IN *CALLITHRIX JACCHUS*

This was an approximate replication of the method used in Study Five, just described, but using common marmoset subjects instead of olive baboons. In this study it was decided that the breeding female of the group would perform as the model. These individuals are dominant in terms of their social role within the group, as discussed in the previous chapter. Furthermore, the food test results with marmosets described in the previous chapter also suggested these animals tend to be dominant in terms of their priority of access to food. In the food test data, none of the

breeding females tested were classed as subordinate to the non-breeding group demonstrator.

This study also differed from the previous one in that extra conditions were introduced in order to investigate whether there was an effect of model number on the strength of any social learning or social facilitation effect found. This was done as it was believed that, in contrast to what was found with the baboons, the presence of a model might actually *facilitate* interaction with the novel object in the marmosets. The affiliative group structure of marmosets suggested that individuals might be *more* inclined to approach a location already occupied by another group member, i.e. a conformity effect might be found. The strength of conformity effects ought to be dependent on the number of models, and indeed such effects have been identified in the literature, commonly referred to as, “positive frequency-dependent social learning” (Day, MacDonald, Brown, Laland, & Reader, 2001). The number of models has been shown to have an effect on the extent of social learning in guppies (Lachlan, Crooks, & Laland, 1998; Laland & Williams, 1997), rats (Galef & Whiskin, 1998), and pigeons (Lefebvre & Giraldeau, 1994). These extra conditions were therefore included to determine whether such an effect could be identified in the marmosets.

METHODS

Subjects

This study involved 46 common marmoset subjects, *Callithrix jacchus*, 21 of which were male and 25 of which were female. These included juvenile, subadult and

adult animals, ranging in age from six months to seven years old. Subjects were taken from the same Medical Research Council population described in the previous chapters. All animals in this study came from a total of 13 family groups and all testing was done within the family group (so that model(s) and observer came from the same home cage).

Thirty animals were assigned the role of observer, and 11 females (each one the breeding female of her group) performed the role of model. Eight non-reproductive individuals (five female and three male) performed the role of second model in the conditions requiring two models (three of the subjects performed as a second model after having been tested as observers).

Apparatus

Again, all testing was done in the animals' home cage, as described in the previous chapters, and shown in Fig. 1 in Chapter Three. A green rubber ice-cube tray (21 x 11 x 2 cm) containing small pieces of marshmallow (the same reward as in Chapters Four and Five with marmosets) was used as the novel feeder.

Training and Habituation

Prior to testing individuals from any one family group, the potential model for that group (reproductive female) was introduced to the apparatus (in isolation in the home cage) on several occasions, until she was reliably feeding from it.

Procedure

Observer subjects were allocated to one of the five conditions such that no condition contained more than one animal from any one family group, and such that each condition had the following subject composition: two breeding males, two non-breeding females and two non-breeding males. See Table 10 for details of the conditions.

Trials would commence when the required combination of individuals from the group had entered the top two sections. Once model(s) were separated from the observer in the top right section of the home cage, the apparatus was introduced and the observation phase began. All trials consisted of an observation phase and a testing phase. During the observation phase, model and observer were separated by the wire mesh dividers in home cage, as shown in Fig. 1 (the observer was simply separated from the novel object in the No Model condition). Each observation phase lasted between 60 and 120 seconds. Following the observation phase, in the Model Removed condition the model was allowed to rejoin the rest of the group in the other sections of the home cage (see Fig. 1). The wire mesh divider was then opened so that the observer was free to enter the demonstration area. In both No Model and Model Present conditions, the wire mesh divider was simply opened immediately after the observation phase. Each testing phase lasted at least 100 seconds, and was timed out after 180 seconds if the subject had failed to approach the apparatus during that time. All trials were videotaped for subsequent coding.

Data Coding

Data coding was done as described in the previous study. However the cut-off point (100s after first approach) was slightly different, again selected such that any differences in terms of remaining quantity of food could not interfere with results. Measurements of particular interest were again i) latency to approach apparatus from time of door release, ii) latency to begin feeding from time of approach, and iii) total duration of contact with apparatus in the coded 100s from first approach. Two subjects failed to approach the apparatus within the trial period, so their data were excluded from the second and third measures.

RESULTS AND DISCUSSION

Figure 21 displays the data for all five of the conditions, for each of the three measures.

Number of Models

No effect of model number was found on any of the three measures, either within the conditions of Model Present and Model Removed, or collapsed across the two conditions. For latency to approach, Mann-Whitney U test: $U=9.5$, $n_1=6$, $n_2=6$, *NS*, for the Model Present condition; Mann-Whitney U test: $U=16.5$, $n_1=6$, $n_2=6$, *NS*, for the Model Removed condition; and Mann-Whitney U test: $U=56$, $n_1=12$, $n_2=12$, *NS*, collapsed across the two conditions. For latency to begin feeding from approach, Mann-Whitney U test: $U=9.0$, $n_1=5$, $n_2=5$, *NS* in the Model Present condition; Mann-

Whitney U test: $U=13$, $n_1=5$, $n_2=6$, NS , in the Model Removed condition; and Mann-Whitney U test: $U=51$, $n_1=10$, $n_2=11$, NS , collapsed across the two conditions. For duration of contact, Mann-Whitney U test: $U=15$, $n_1=6$, $n_2=6$, NS , in the Present condition; Mann-Whitney U test: $U=18$, $n_1=6$, $n_2=6$, NS , in the Removed condition; and Mann-Whitney U test: $U=66.5$, $n_1=12$, $n_2=12$, NS , collapsed across the two conditions. As model number appeared to have had no effect on the results, further analysis collapsed data from One Model and Two Model conditions.

Effects of Model Presence

Latency of approach showed a significant overall difference between the three conditions (Kruskal-Wallis test: $H_2=7.096$, $P<0.05$). However, the other two measures showed no overall difference (for latency to feed, Kruskal-Wallis test: $H_2=4.130$, NS ; and for duration of contact, Kruskal-Wallis test: $H_2=0.666$, NS).

There was clearly an effect of having seen the model, however, as post-hoc tests showed that the Model Removed group were significantly faster to approach than the No Model group ($P<0.05$). Furthermore, this effect did not appear to be masked in the Model Present condition, as it had been in the baboons. Subjects from the Model Present condition were not significantly slower to approach the apparatus than those from the Model Removed condition, although they were also not significantly quicker than those from the No Model condition. However, as noted in the data coding section, two animals failed to approach during the allotted time period. Both of these individuals were from the No Model group, which meant that, in the case of the

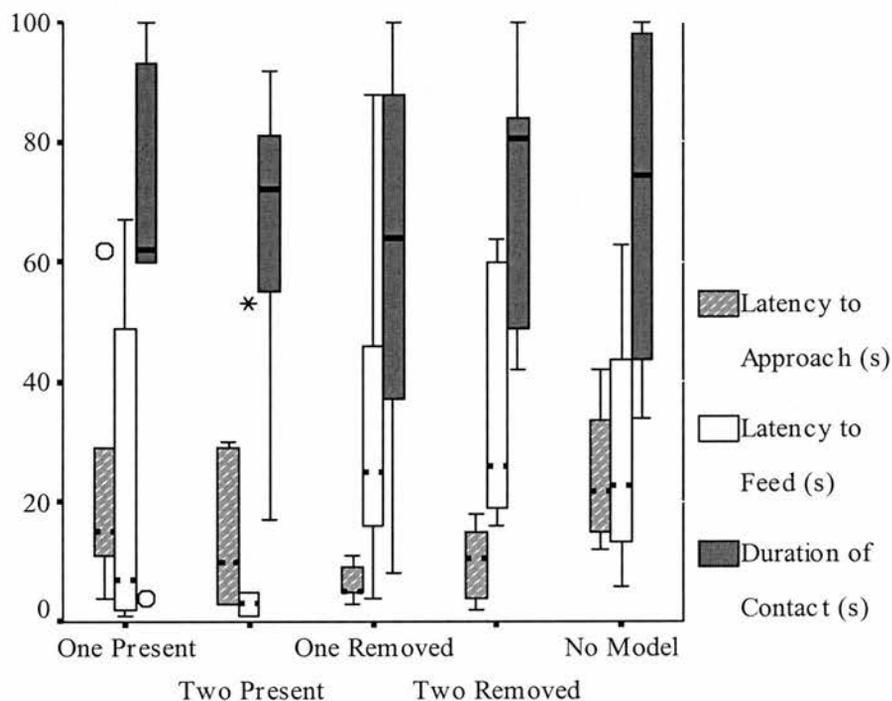
marmosets, seeing a model made approaching significantly more likely ($\chi^2 = 8.571$, $df = 1$, Fisher's Exact Test: $P < 0.05$).

Three of the subjects that did approach failed to eat anything during the trial period, one from the Model Removed condition, and two from the Model Present condition. This difference was not significant ($\chi^2 = 0.381$, $df = 1$, Fisher's Exact Test: *NS*). The measure of latency to feed, although not quite significant across the conditions according to the Kruskal-Wallis test, as noted above, did provide some evidence that the continued presence of the model might actually enhance the effects of social influence in the marmosets. Using a one-tailed Mann Whitney test (given the predictions made in the introduction), a significant difference could be found between the Model Present and Model Removed condition on this measure, with those in the Model Present condition being faster to begin feeding from the novel object upon approach (Mann-Whitney *U* test: $U=28$, $n_1=10$, $n_2=11$, $P < 0.05$, one-tailed).

Thus it appeared that, like the baboons, the marmosets showed some clear signs of having been influenced by the observation of a model. Observation of the model appeared to have promoted their interactions with the novel object. However, contrary to what had been found in the baboons, it appeared that this effect was not masked when the dominant model was still present, and in fact there was weak evidence that such effects might be amplified when the model was present.

Figure 21. – Behaviour towards a novel object for marmoset subjects from the five groups:

One Model Present (in which a dominant model was present before and during the test period); Two Models Present (in which a dominant model and a non-dominant model were present before and during the test period); One Model Removed (in which a dominant model had been observed, but was released before the test period); Two Models Removed (in which a dominant model and non-dominant model had been observed, but were released before the test period); and No Model (in which no model was observed at any time).



Key:

- Median
- Box length Interquartile range
- Whisker Range, excluding...
- o Outliers, between 1.5 and 3 box lengths from the median
- * Extremes, over 3 box lengths from the median

Figure 22. - Latency to approach novel object (mean \pm standard error) for marmosets and baboons in the Model Present, Model Removed and No Model conditions

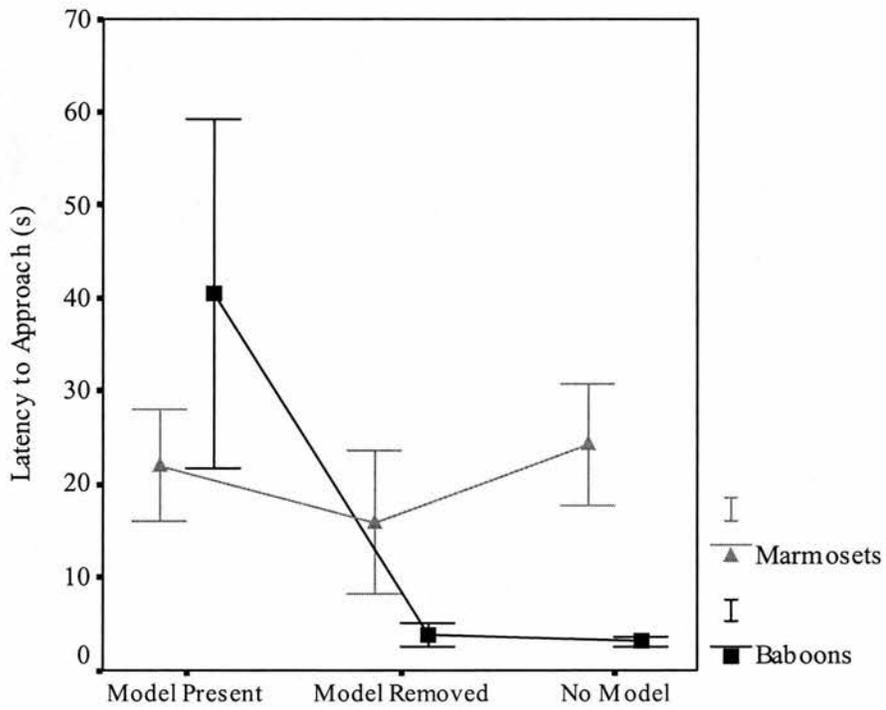


Figure 23. - Latency to feed from novel object (mean +/- standard error) for marmosets and baboons in the Model Present, Model Removed and No Model conditions

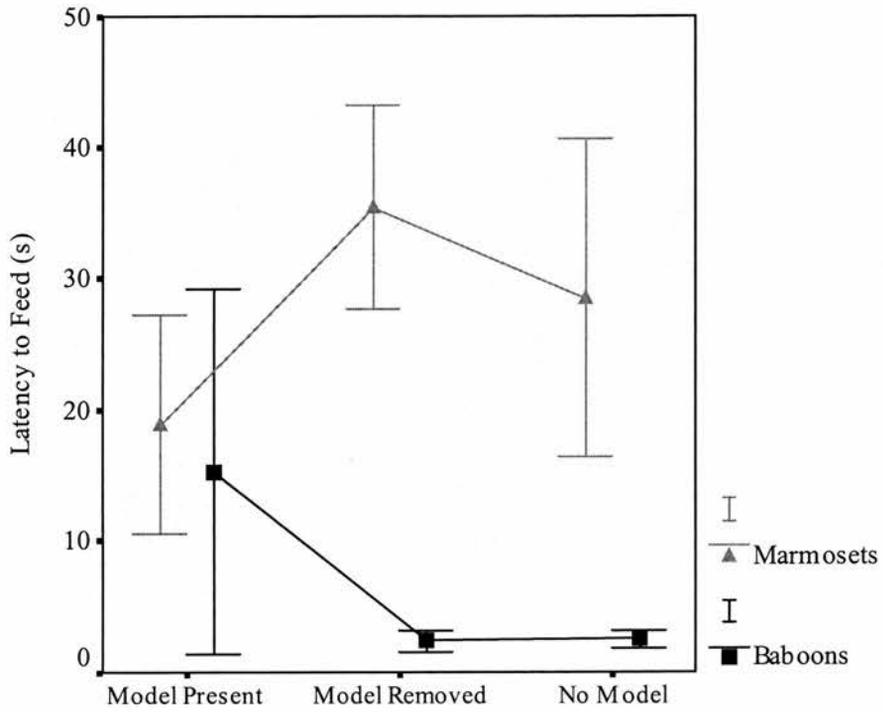
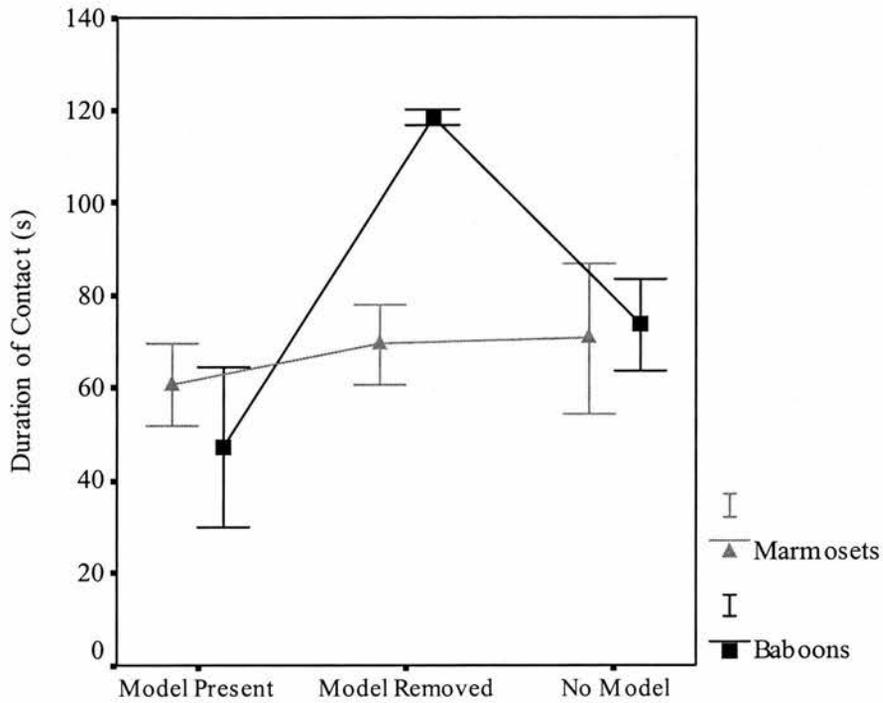


Figure 24. – Duration of contact with novel object (mean +/- standard error) for marmosets and baboons in the Model Present, Model Removed and No Model conditions



General Discussion

Whilst direct comparisons between the performance of the baboons and marmosets would be somewhat imprudent, it is clear that the overall patterns of behaviour when the three groups are considered are very different. Figures 22, 23 and 24 plot the data for the marmosets and baboons on the same axes such that these different patterns can be more easily discerned. Figure 22 displays the data for latency to approach, and as can be seen, the slight enhancement effect shown by the marmosets as a result of seeing a model, contrasts strongly with the pattern observed in the baboons, where the control group were actually quicker to approach than those that could interact jointly with the dominant model. Figure 23, which shows latency to feed, a measure which did not show great differences between the groups for either species, presents an unexpectedly powerful depiction of the contrast between the two. Whilst there was some evidence that the marmosets were particularly quick to begin feeding under the Model Present condition, those from the equivalent baboon group were the slowest of the three groups.

Figure 24, displaying the data on the duration of contact with the novel object, is perhaps most relevant of all, indicating as it does how inclined the animals were to interact jointly with the model. For the marmosets, there were no differences between the groups; each spent as long interacting with the apparatus as the others. However, for the baboons, despite the fact that having seen a model *previously* interact with the object induced them to perform at ceiling level (staying in contact with the novel object for the entire coded period), those from the Model Present condition spent the *least* time of each of the groups interacting with the apparatus. This would suggest

that, as has been suggested in the previous literature, joint interaction between a dominant model and a subordinate learner is hindered by social constraints.

Clearly, therefore, there are considerable obstacles to transmission of skills from dominant model to subordinate learner. As pointed out by Visalberghi & Frigaszy (1990), even if they had picked up some information about an object from observing another individual, subordinates would rarely get the opportunity to interact with such desirable objects, which could potentially allow them to learn more detailed skills through trial and error. Furthermore, due to their inhibition from approaching more dominant individuals, there would be few opportunities for joint interaction, reducing the possibilities for the more detailed learning of skills in this, probably more efficient, way. Such barriers to information transfer could potentially drive directed social learning.

As in the previous chapter, any such barriers to social transmission were considerably less evident within the marmoset population tested. Such contrasts provide strong support for the suggestion made by Coussi-Korbel & Frigaszy (1995) that directed social learning would be a pattern more typical of steeply hierarchical societies. In contrast, tolerant egalitarian groups would be expected to show non-specific social learning, with skills being more readily, and more uniformly, transmitted.

The results from this chapter also support the suggestion made by Visalberghi & Frigaszy (1990) that cognitively complex social learning abilities in monkeys may be masked due to the influence of social constraints. Although the baboons' interest in

the apparatus was clearly heightened in the Model Removed condition (indicating that they were certainly susceptible to some level of social influence) their performance when the model was still present suggested that there would have been greater opportunities for them to learn in an entirely non-social situation.

Chapter Seven

SOCIAL LEARNING AND THE INFLUENCE OF SOCIAL CONTEXT

Methodological Issues

The data and arguments presented in the thesis have many implications. However, before these are addressed, it is important to deal with certain methodological issues relevant to the empirical work. As noted in Chapters Five and Six, considerable differences were found between common marmosets and olive baboons in terms of their responses to comparable social situations, and it is proposed that these differences can be attributed at least in part to the differences in social style between the two species. In both chapters, however, caution was urged in this interpretation, as the differences could have arisen due to other sources of variation between the groups, either in terms of some other kind of species difference, or in some minor (but crucial) difference in procedure between the replications.

One such difference between the baboon and marmoset studies arose from the demographics of the two samples. The marmosets, tested as they were within their family group, ought to have provided a sample highly representative of the population as a whole, including both male and female subjects from a broad age range. However, the baboon experiments were carried out within an entirely juvenile sample, and in one of the experiments (Study Three) all subjects were juvenile males. Testing was carried out in this manner for very good reasons; previous pilot work carried out

within our research group indicated that adult subjects were much less eager to enter the testing cubicles, principally due to their greater distraction by the surrounding social environment, which we assumed could be mainly attributed to sexual interest. Therefore, although the selection of a juvenile sample made testing viable, it also clearly made the results less representative of the population.

However, these sampling differences probably do not threaten the interpretation of the studies in Chapters Five and Six, given their outcome. As shown in Chapter Five, the differences in demonstrator behaviour were found in the baboons, not the marmosets. The narrower sample of baboons could lead one to conclude that such social effects might be *less* pronounced in this group, but not more so. Although Chapter Six showed some positive effects for both samples, the effects found in the baboons were apparently stronger. Furthermore, the fact that the baboons and marmosets appeared to be influenced in opposite directions (inhibition versus possible facilitation) by the presence of the model, ought not to be affected by the broadness of one sample in relation to the other.

Of course, it could be the case that the relatedness of model and observer in the marmosets created a difference between their performance and the performance of the (probably only distantly related) baboons. Such differences are however entirely relevant to the issue of how social structure affects social learning. Marmosets were tested within their family groups as this is their natural group structure, and baboons were tested with individuals that were only loosely related for similar reasons. It would nonetheless be extremely interesting to study the behaviour of baboons that

were known to be closely related (mother and infant, for example) under similar conditions.

As was stated in Chapter Five, the proposed interpretation of the influence of social structure would be considerably strengthened if similar contrasts could be found between further pairs of species with similarly contrasting social structures. As noted in Chapter Two (with regard to making comparisons of species cognitive ability) this reduces the possibility of “contextual variables”. However, the results of Chapters Five and Six together already present a fairly strong picture. Firstly, in each chapter, predictions were made about how each species would perform on the basis of their social structure, and by and large these were supported. The baboon demonstrators showed much greater sensitivity to the relative dominance of their observer, performing more hesitantly when the observer was dominant to themselves (Study Three). The marmoset demonstrators showed no such variation (Study Four). The baboon observers were inhibited from approaching a dominant model (Study Five), whereas the marmoset observers appeared to benefit from such a situation (Study Six). As noted in Chapter Two, when making species comparisons, it is of crucial importance to make predictions that are directional and predictive, rather than attributing post-hoc interpretations to existing data sets. Secondly, since the effects found in Chapters Five and Six do appear to be, in essence, social ones, alternative interpretations not involving some kind of social difference between the two populations would seem unlikely.

Directed Social Learning

In Coussi-Korbel & Fragaszy's (1995) review, *On the relation between social dynamics and social learning*, it was stated that those species with despotic social structures would tend to show patterns of directed social learning, and those with more tolerant social structures would show more non-specific social learning. Coussi-Korbel & Fragaszy (1995) went on to conclude that behavioural variability would be more common within despotic populations, whereas tolerant populations would be characterised by a much greater degree of behavioural homogeneity.

The work presented in this thesis therefore provides support for the first of these assertions: that directed social learning may be more common within a despotic population. However, the second proposal, regarding behavioural variability, remains a supposition for the time being. Testing this hypothesis will depend on the results of more naturalistic experiments, in which novel tasks are introduced into a number of groups, so that the influence of particular types of social structure on transmission can be discerned. As yet, only two authors have carried out research comparing transmission patterns between different species. Cambefort (1981) presented a number of feeding tasks (involving “clues” which indicated where food was hidden) to a group of chacma baboons, *Papio ursinus*, and a group of vervet monkeys, *Cercopithecus aethiops*. From the data, it could be concluded that baboon innovators were typically juveniles, and the rest of the baboon troop learned extremely quickly following the first discovery. In the vervet monkeys, the new habits spread through the troop via a much wider variety of social channels, and propagation was much slower. Cambefort (1981) notes that the baboon social structure is very hierarchical compared with vervet groups, and certainly the pattern found appears to suggest that

social learning in the baboons was more directed. However, further comparisons are required before conclusions can be drawn about whether *any* group with these social structures will show in similar patterns of social transmission. Beck (1972; 1973a, 1973b, 1976) also used a similar kind of comparative design, although the intention was to investigate cognitive, as opposed to social, differences. He presented a food-raking task to two different species of baboon, and one macaque species. The behaviour appeared to spread much more rapidly within the macaque group, compared with the baboons. Beck's (1976) conclusion was that macaques were more adept social learners than baboons, and in support of this interpretation, mentioned also that anecdotal reports of macaque behavioural traditions have been common, whereas baboon innovations have typically involved only one individual. However, both differences could equally have resulted from the differing social styles of the species involved.

Clearly, if this area of research is to be extended to apply to a wide variety of species, some kind of metric for despotic/hierarchical versus tolerant/cooperative is required. Coussi-Korbel & Fragaszy (1995) suggest that these concepts could be quantified in terms of the degree of asymmetry characteristic of dyadic interactions within the species. The amount of asymmetry can be calculated in terms of any dominance behaviours typical of the species under consideration, including basic approach and retreat interactions. This seems to be a particularly good measure, in that it ought to be calculable for virtually any species, including those outwith the primate family. If the results presented in this thesis can be extended to a wider variety of species, we would therefore expect the marmoset pattern (facilitation of learning in the presence of other individuals) to occur when dyadic interactions are

relatively symmetrical, and the baboon pattern (inhibition of learning due to demonstrator inhibition and a lack of joint interaction) when interactions are biased towards asymmetry.

The notions of dominance and asymmetry may also be relevant for predicting when scrounging behaviour is liable to facilitate, rather than inhibit learning. Brown, Almond, & van Bergen (submitted) have distinguished two broad categories of food transfer; transfer which is predicted by dominance relationships, and transfer that occurs for other reasons, such as trade, reciprocity or kin selection. Given that marmosets are known to share food with infant group members, the “scrounging” that occurred in Study Two may be crucially different from the exploitative scrounging that has typically inhibited learning in previous studies. It may therefore transpire that scrounging will also facilitate learning in other species that exhibit less asymmetrical modes of food transfer.

It should also be noted however that a pattern of directed social learning can arise from many sources other than dominance. Familiarity with a demonstrator has been identified as one factor which can influence the efficacy of social learning. This has been demonstrated in guppies by Swaney, Kendal, Capon, Brown, & Laland (2001), who found that their subjects learned a route to a food source more quickly when the trained demonstrator fish was familiar to them, compared with an unfamiliar fish. Chesler (1969) found a similar effect in kittens learning a discrimination lever press response. The kittens acquired and discriminated the response faster when the demonstrator was their mother, compared to an unfamiliar cat.

There is also evidence that some animals may preferentially attend to 'good' demonstrators, on the basis of prior experience. As noted in Chapter Five, Nicol & Pope (1999) found that dominant hens were the most effective demonstrators in an operant discrimination task. Nicol & Pope (1999) proposed that this may have been due to the greater foraging success of these individuals. They attempted to test this interpretation by manipulating perceived prior foraging success. A two-week pre-testing period was introduced, during which demonstrators were seen by the subjects to be foraging either successfully (finding prized food items in their enclosure) or unsuccessfully (finding no food). This manipulation did not appear to disrupt the basic effect of dominant demonstrators as the most effective. However, as Nicol & Pope (1999) note, this could be because this short-term learning period was not sufficient to offset the flock's long-term experience of their demonstrator's foraging success.

A similar proposal was made by Fritz, Kemps, Voelkl, & Huber (2002) who found that one of their marmosets was apparently more effective than another as a demonstrator in an artificial prey-capture task, despite the virtually identical demonstration performance of the two. Since the more effective demonstrator had previously been documented as the innovator of a novel skill which was subsequently learned by the rest of the group (reported in Voelkl & Huber, 2000), Fritz et al. (2002) cautiously attribute the difference in the groups' performances to their greater attention to this demonstrator, on the basis of her prior significance as a model.

Theoretical and Practical Implications

Directed social learning has implications for theoretical models of trait diffusion within populations, such as those described by Laland, Richerson, & Boyd (1996). Laland et al. (1996) note that models of biased transmission (influenced by such factors as demonstrator preference and opportunities for scrounging) may result in somewhat counterintuitive predictions about transmission, such as a non-accelerating rate of diffusion. As mentioned in Chapter One, the non-accelerating rates of behavioural diffusion within macaque populations were interpreted by Lefebvre (1995a) as indicative of asocial learning (independent discovery), rather than social transmission. Given Laland et al.'s (1996) proposals, Lefebvre's interpretation may not necessarily be accurate.

Social context effects on social learning may also have considerable practical implications. As noted in Chapter One, social learning may be relevant for pre-release training for reintroductions. Reviews by Brown & Laland (2001) and Custance et al. (2002) stress the potential role of social learning in reintroductions of hatchery-reared fish and captive-bred primates respectively. In each of these articles, the authors suggest that any such program would benefit from judicious selection of both demonstrator and group composition. In order to make such decisions, it is clear that further research on directed social learning (and in particular, how these patterns may differ between species) is crucial.

Beck (1997) has proposed that social learning could be incorporated into a pre-release training program for primate reintroduction by capturing an already

successfully reintroduced individual and integrating it with a naïve group. The main recommendation that could be taken from this thesis therefore, would be to ensure that such an individual was selected primarily on the basis of its likelihood of forming a tolerant relationship with at least one of the members of the training group.

Although infants are liable to be tolerated, they are of course unlikely to have developed all of the life skills that a demonstrator must essentially possess. It is more likely that the best individual for this role would be an adult that could be readily incorporated into the group as a sexual partner. Thus, group composition will also be important as, in the case of the marmosets for example, this would be unlikely to occur if the naïve group were a complete family unit.

DO MONKEYS APE?

What are the implications of the social context effects identified in this thesis for assessing the relative social learning skills of monkeys compared with other animals? Prior to addressing the issue of whether or not the reputation of monkeys as poor social learners is justified, it is important to establish how they developed this reputation in the first place. Visalberghi & Fragaszy (1990) and Visalberghi & Fragaszy (2002) together review a total of seventeen published reports and a number of further unpublished studies, many of them from their own research groups. In both of these papers the authors conclude, as noted in previous chapters in this thesis, that monkeys do not make use of imitation as a learning mechanism, and probably do not possess the requisite representational abilities to do so. The studies they cite span a

range of contexts, including tool use, manipulative puzzles, spontaneous imitation and attempts to elicit imitation through training. These will be briefly reviewed below.

Tube tests

Fragaszy & Visalberghi (1989), Visalberghi & Trinca (1989) and Visalberghi (1993) have all attempted to investigate whether capuchin monkeys (known for their tool use in both their natural habitat and in captivity) could learn by observation to use a stick tool to probe a narrow transparent tube in order to obtain a food reward. In each case, the task was presented to an entire group, and the aim was to determine whether observing an individual that had perfected the skill facilitated solution by observers. Since some individuals witnessed many solutions without developing the skill themselves, Visalberghi & Fragaszy (1990) and Visalberghi & Fragaszy (2002) concluded that imitation could not be involved.

Other tool use tasks

Westergaard & Fragaszy (1987) presented similar problems to a group of capuchin monkeys. In one study, they were given the opportunity to sponge juice from a hollow, and in the other the group were given sticks which they could insert into a syrup-filled recess. In both cases, the majority of the nine capuchin subjects developed the behaviour, and in each of the studies there was evidence for conspecific observation leading to solution in at least one individual. Notably, in the syrup stick experiment, the first infant of the group to acquire the behaviour was one who had observed her mother very closely, sharing the food reward and occasionally holding the tool at the same time. However, as Visalberghi & Fragaszy (1990) note, this does

not represent conclusive evidence of imitation. A later syrup stick experiment with lion-tailed macaque subjects (Westergaard, 1988) showed similar results: a naïve animal rapidly acquired the behaviour on being exposed to two skilled conspecifics (much faster, that is, than the speed at which these initial solvers had discovered the technique). But again Visalberghi & Fragaszy (1990) urged caution in the interpretation of this result, pointing out that no firm conclusions can be drawn about the process involved.

As with the tube tests, there have been several attempts to investigate the social transmission of nut-cracking behaviour in groups of capuchin monkeys. Visalberghi (1987), Fragaszy & Visalberghi (1989) and Antinucci & Visalberghi (1986; cited in Visalberghi & Fragaszy, 1990) all attempted to elicit nut cracking behaviour, involving the use of a tool. Again, the tasks were presented to groups of capuchin monkeys, but with little evidence of observational learning. In two of the groups studied, only one individual ever became proficient and, despite this animal then performing the behaviour on many occasions in view of the group, no further monkeys adopted the behaviour. In the other group studied, five individuals became solvers, but again Visalberghi & Fragaszy (1990) took the lack of a relationship between observation and solution as evidence against imitation having played a role in learning.

Beck (1972; 1973a, 1973b, 1976), mentioned earlier in this chapter, investigated the social transmission of raking behaviours in Guinea baboons, hamadryas baboons and pigtailed macaques. Groups of these animals were presented with sticks with which they could rake in food rewards that were otherwise out of reach. Although the

baboons did not appear to be facilitated towards the solution by watching a skilled individual, there was considerable evidence for some kind of social learning in the macaques. Beck (1976) notes in particular that the dominant male of the group appeared to use the exact same raking technique as the first solver. However, Visalberghi & Fragaszy (1990) again stress the difficulties of interpreting data such as this.

Puzzle Feeders

A number of studies have endeavoured to identify imitative learning in monkeys through the use of some kind of manipulative task, the solution for which results in a food reward. In a similar manner to many of the studies cited above, Adams-Curtis (1987) presented a puzzle feeder such as this to a group of capuchin monkeys. The puzzle required that a number of latches were released in a specific sequence. Although one individual learned to obtain food from this apparatus, none of the other group members developed the behaviour. Observation of the skilled individual did not appear to have any effect in terms of bringing the general manipulations of the observers any closer to the correct sequence.

More controlled methodologies have also been employed however. As noted in previous chapters, Custance et al. (1999) presented capuchin monkeys with an “artificial fruit”. Using human demonstrators and a two-action design, this study was able to show that the subjects *were* influenced by the particular demonstration that they had seen, and produced solutions more like the version they had seen modelled. Visalberghi & Fragaszy (2002) note that this could nonetheless be attributed to

“object movement re-enactment” (as discussed in Chapter Two) and as such, does not represent evidence of imitation.

In another study mentioned previously (Chapter Three), Bugnyar & Huber (1997) used an approximation of the two-action method. Visalberghi & Fragaszy (2002) again note that the observed difference between the two groups could be a result of object movement re-enactment.

Visalberghi & Fragaszy (2002) cite a further two-action experiment involving monkey subjects (Gardner, Visalberghi, & Heyes, submitted, cited in Visalberghi & Fragaszy, 2002). This study employed the bi-directional control procedure, first used to test for imitation in rats (Heyes & Dawson, 1990). Two monkey demonstrators were each trained to push a manipulandum either to the left or to the right for a food reward. Subjects were allowed to see one of these versions. Although initial testing (in which subjects *faced* the demonstrator during observation) showed no evidence of behaviour matching, subsequent testing (in which subjects joined the demonstrator in the same cage during observation) found that seven out of the eight subjects tended to push in the same direction as their demonstrator. Visalberghi & Fragaszy (2002) suggest that this is a clear case of object movement re-enactment, given that matching only appeared possible when egocentric and allocentric axes matched (i.e. no perspective transformation was required).

Spontaneous Imitation

The first attempt to elicit spontaneous imitation in monkeys was published by Hervé & Deputte (1993), who studied the influence of a human demonstrator on a human-raised capuchin monkey. It was found that although the monkey was clearly subject to social influence effects inasmuch as it contacted the same objects as the demonstrator, it did not match the demonstrator's *actions* on the objects with any regularity.

In addition to this, Visalberghi & Fragaszy (2002) also cite two further attempts to document spontaneous imitation in monkeys. Perucchini, Bellagamba, Visalberghi, & Camaioni (1997) replicated a study originally carried out on young children (Camaioni, Baumgartner, & Pasucci, 1988, also cited in Visalberghi & Fragaszy, 2002) which looked at imitation between pairs of children during play. Visalberghi & Fragaszy (2002) report that although imitation of actions on objects was common in children, it was completely absent in the capuchin pairs. Like the Hervé & Deputte (1993) study, however, the monkeys showed evidence of interest in the same objects (attributed to stimulus enhancement), and also some evidence of social facilitation of common behaviours. Finally, Visalberghi & Fragaszy (2002) report on several occasions attempting to elicit neonatal facial imitation (similar to that reported by Meltzoff & Moore (1983) in human infants) in their newborn capuchins, and note that such attempts have so far proven unsuccessful.

Training to Imitate

Like the Do-as-I-do imitation experiments with chimpanzees (mentioned in Chapter Two, p43), there have been a number of attempts to elicit imitation in monkeys in the same manner. Mitchell & Anderson (1993) provided food reinforcement to a long-tailed macaque for producing scratching behaviour when a human model scratched. Discrimination training was later given such that the subject was only rewarded for scratching the same body area as the model. However, although there was some suggestive evidence that the monkey had learned the location discrimination based on the four trained body areas, there was no evidence for generalisation to new body areas. Hemery, Frigaszy, & Deputte (1998, cited in Visalberghi & Fragaszy, 2002) tried a different approach, rewarding three human-raised capuchin monkeys for matching the behaviour of a human demonstrator in actions on their own bodies, actions on an object, and actions involving a combination of objects. The most proficient subject was later tested using novel modelled actions. Visalberghi & Fragaszy (2002) report that independent coding showed the subject to have matched the action on 12.5% of the trials. It is hard to judge purely on the basis of this statistic whether or not these actions were sufficiently improbable to provide support for imitation. However, Visalberghi & Fragaszy (2002) go on to describe an attempt to determine a baseline rate of the actions that had been reproduced, by providing the test materials to a group of untrained monkeys. Actions like the ones seen during testing were only produced at a very low baseline probability, leading Visalberghi & Fragaszy (2002) to conclude that, “it seems unlikely that the subject produced even three partial matches [which together accounted for the 12.5% statistic] fully by chance.”

Interpreting the Literature

Certainly, the results of these studies, viewed as a whole, do not paint a particularly promising picture for monkey imitative abilities. However, in the light of the material presented in this thesis, it becomes clear that some of the negative results reported in the previous literature should not necessarily be taken at face value.

Firstly, there is the issue of testing in groups. In many of the studies (twelve out of the seventeen published articles) mentioned above, testing was done within a social group, simply by introducing the apparatus and effectively collecting purely observational data from then on.

Group testing can result in a whole range of social effects that may mask social learning. As noted in Chapter Four, scrounging behaviour has frequently been identified as having an inhibiting effect on social learning, with monkeys being no exception (Fragaszy & Visalberghi, 1989). However, although group testing will inevitably lead to the kind of economic interaction between producers and scroungers discussed in Chapter Four, this does not necessarily mean that the scroungers have learned nothing from their proximity to the producers. Very few of the subjects in Study Two became producers during their interactive observation period, but following this type of observation, nearly all went on to master the skill for themselves.

Furthermore, although Visalberghi & Fragaszy (2002) have stressed the generally tolerant social interactions within capuchin monkey groups (the species on which many of these group studies have focussed), it is clear that the social

constraints described in this thesis concerning baboons, also apply at least to some extent, to capuchins. Frigaszy & Visalberghi (1990) review some of their research groups' studies in terms of the social processes which they understood to have influenced the development and spread of novel behaviours. In addition to identifying exploitation of a producer as an obstruction to social learning, they also mention inhibition of performance as a factor which often impeded the spread of a new skill: "a proficient individual can be completely inhibited from displaying a particular skill, even in the absence of obviously threatening interactions. Stated simply, performance is not indicative of competence, and social factors can be responsible for the dissociation." (Frigaszy & Visalberghi, 1990, pp159-160). This description seems closely analogous to the phenomenon illustrated in Chapter Five. Frigaszy & Visalberghi (1990) do not mention specifically that *naïve* individuals were inhibited from approaching skilled demonstrators (which would be analogous to the behaviour of the baboons in Chapter Six), but they do note that the single case of coercion that they documented appeared to strongly facilitate learning (the instance of an infant using a tool to obtain syrup, from Westergaard & Frigaszy (1987), described above).

A further problem with the kind of group testing reported in these various studies is that firm conclusions of *any* kind, as regards the nature of the mechanisms involved, are virtually impossible. In a number of the studies described above, there was relatively strong suggestive evidence of observational learning. However in each case the authors (rightly) stress the difficulties associated with making such interpretations from this kind of data.

Group testing of this sort has been particularly common in studies of social learning in monkeys compared with those carried out in other phyletic groups. The smaller subject numbers involved in great ape studies have usually entailed individual testing, and often the demonstrators have been human (effectively eliminating the problem of demonstrator performance variations). And laboratory species such as birds and rats have typically been tested in much more controlled conditions all round (and when group testing *has* been done in lab species, it is clear they can be subject to the same inhibitory effects: see the discussion of Giraldeau & Lefebvre (1987) in Chapter Four). The extensive body of research into social transmission within groups of monkeys has therefore resulted in a proliferation of negative results. To some authors this typical absence of evidence for monkey imitation has been taken for evidence of absence. For example, the review by Lefebvre & Bouchard (in press), mentioned in Chapter One, employed the systematic review methodology briefly mentioned in Chapter Two (reviewing the total number of published reports of social learning in each species, without evaluating the methodology of those studies). They note that for monkeys in particular, many studies of imitation have returned negative results, whereas all bird species that have been tested have shown positive evidence of imitation.

When the details of the studies' methodology are taken into consideration, however, an altogether different picture of monkey social learning abilities appears to emerge. As noted in Chapter Two, the use of analogous procedures for testing for imitation across species provides a particularly powerful window to the relative social learning abilities of those species. In general, when monkeys have been tested using a procedure which has previously obtained positive results in another species, the

findings have been extremely promising. For example, Voelkl & Huber (2000), described in Chapter Three, (although not reviewed in Visalberghi & Fragaszy, 2002), used a hand/mouth two-action design with marmoset subjects, similar to many of those carried out with bird species (e.g. Zentall et al., 1996). A clear difference between the two observer groups was found. Similarly, the results of Study One (also with marmosets) showed clear differences between the groups, and although this is arguably not evidence of imitation (see Discussion section, Chapter Three), it is at least as convincing as one of the bird examples that Lefebvre & Bouchard (in press) class as positive evidence of imitation (Palameta & Lefebvre, 1985).

Visalberghi & Fragaszy (2002) cite an attempt to elicit imitation in their capuchin monkeys using the bi-directional control procedure, a methodology which has previously achieved positive results when used with rat subjects (Heyes et al., 1992; Heyes & Dawson, 1990). However, considerable replication and re-analysis of the rat experiments suggest that the interpretation of object-movement re-enactment attributed to the monkeys may also be appropriate for the rats (e.g. Campbell & Heyes, 2002; Ray, Gardner, & Heyes, 2000).

Methodologies first employed with great apes have also proved successful when tested on monkey subjects. Although the Custance et al. (1999) artificial fruit experiment with capuchin monkeys could be attributed to object movement re-enactment, the same criticism can (and has) been levelled at the chimpanzee version reported in Whiten & Custance (1996) (see Heyes & Ray, 2000). Again, the results of Chapter Three are relevant here, also having made use of the artificial fruit methodology. Between-group differences were found despite the limited manipulative

competence of marmosets (although see Chapters Two and Three for why this particular version was not a perfect replication of the chimpanzee and capuchin experiments).

Visalberghi & Fragaszy (2002) note that the capuchin they trained to imitate on command had particular difficulty matching actions on the body (which is consistent with Mitchell & Anderson's (1993) failure to find this type of imitation in a macaque). However, in Myowa-Yamakoshi & Matsuzawa's (1999) analysis of which actions are most readily imitated by chimpanzees, the same pattern emerged. Both chimpanzees and capuchins appear better able to match actions on objects.

The failed attempts to elicit neonatal facial imitation in infant capuchin monkeys may suggest that chimpanzees have an imitative edge over monkeys, given that Myowa (1996) reports imitation of facial gestures in a newborn chimpanzee. However, since this result is yet to be replicated in any more than this one subject, and given that even the research on human neonatal imitation is not without its critics (e.g. Anisfeld, 1996; Jones, 1996), it would almost certainly be premature to draw such a conclusion.

The only species with which monkeys have so far compared poorly is in fact *Homo sapiens*. Whilst Perucchini et al. (1997) found little evidence of spontaneous imitation within capuchin pairs, Camaioni et al. (1988) had found that children imitated each other's activities extremely readily, including unusual actions. Modena & Visalberghi (1998, cited in Visalberghi & Fragaszy, 2002) presented a version of the tube test (previously used with capuchins) to children of up to two years of age.

Those over 15 months old (although not younger) performed significantly better if they had seen an adult demonstration. It is no surprise however that monkeys do not appear to imitate quite as readily or proficiently as human children. It has been suggested that humans may represent a special case within the animal kingdom in terms of their imitative proclivities, possibly even possessing something akin to an innate drive to imitate (e.g. Blackmore, 1999; Meltzoff, 1988; Tomasello, 1999, and see Whiten et al., in press, for an example showing that children can be less selective in their imitation than chimpanzees).

However, it is clear that, in relation to other non-human species, the imitative abilities of monkeys are nowhere near as poor as a cursory perusal of the literature might lead one to believe. So are monkeys truly the irrepressible copycats of popular belief? Almost certainly not. There is still no evidence to suggest that monkeys may be any *more* talented as social learners than any other particular phyletic group, and much of the everyday social learning done by monkeys may well rely on the simplest of mechanisms. One conclusion is clear however: the respective myths of monkeys as mimics and as mavericks have together spawned an abundance of fascinating literature.

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Appendices

**APPENDIX 1. - STUDY ONE INDEPENDENT CODERS' RATING
SHEET**

Marmoset Imitation Study

Clip Number and Time:

Subject and Trial:

Comments:

Rater:

Hand	Lid	Bolt-holes	
		Top of lid	
	Handle	Top	
		Shaft	
		Bottom	
		Turn (from top)	
		Turn (from bottom)	
	Other part (e.g. side walls)		
Mouth	Lid	Bolt-holes	
		Top of lid	
	Handle	Top	
		Shaft	
		Bottom	
		Turn (from top)	
		Turn (from bottom)	
	Other part (e.g. side walls)		

**APPENDIX 2. – STUDIES THREE AND FOUR INDEPENDENT
CODERS' RATING SHEET**

Clip Number and Time:

Observer Identity:

Same/Different

Cage

Comments:

Rater:

A. Ratings of observer's behaviours

1. How much attention did the observer appear to be paying to the demonstrator?

1	2	3	4	5	6	7
Paid no attention			Paid very close attention			

2. How much of the demonstration did the observer see?

1	2	3	4	5	6	7
Saw very little			Saw all demos in great detail			

3. To what extent did the behaviour of the observer actively prevent the demonstrator from performing (e.g. hogging/defending apparatus, threatening behaviour)?

1	2	3	4	5	6	7
Not at all			A great deal			

B. Ratings of demonstrator's behaviours

4. How closely did the demonstrator monitor the behaviour of the observer?

1	2	3	4	5	6	7
Totally oblivious			Very closely			

5. Did there seem to be a relationship between the attention of the observer and the timing of the demonstrations, i.e. did demonstrations appear to be performed selectively, when the observer's attention was elsewhere?

1	2	3	4	5	6	7
No apparent relation			Very obvious relation			

Comments: