

VISUAL PROCESSING IN A PRIMATE TEMPORAL
ASSOCIATION CORTEX: INSENSITIVITY TO SELF-
INDUCED MOTION

Jari K. Hietanen

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ABSTRACT

An animal's own behaviour can give rise to sensory stimulation that is very similar to stimulation of completely external origin. Much of this self-induced stimulation has little informative value to the animal and may even interfere with the processing of externally-induced stimulation. A high-level association area in the temporal cortex of macaque (superior temporal polysensory area, STP) which has been shown to participate in the analysis of visual motion was targeted in a series of experiments in order to investigate whether this brain area discriminates externally- and self-induced stimulation in its visual motion processing. Earlier results in somatosensory processing within this same brain area provided grounds for this presumption

The cells studied in here were sensitive to the presence of motion but showed no selectivity for the form of the stimulus. 25% of all visually responsive cells in area STP were classified as belonging to this class of cells. This group of cells was further categorized into unidirectional (39%), bidirectional (4%) and pandirectional (57%) cells. Tuning to direction varied in sharpness. For most cells the angular change in direction required to reduce response to half maximal was between 45 and 70 degrees. The optimal directions of cells appeared clustered around cartesian axes, (up/down, left/right and towards/away). The response latency varied between 35.0-126.4 ms (mean 90.9 ms). On average cell responses showed a transient burst of activity followed by a tonic discharge maintained for the duration of stimulation. 83% of the motion sensitive cells lacking form selectivity responded to any stimuli moved by the experimenter, but gave no response to the sight of the animal's own limb movements. The cells remained, however, responsive to external stimulation while the monkey's own hand was moving in view. Responses to self-induced movements were recovered if the monkey introduced a novel object in its hand into view. That the response discrimination between externally- and self-induced stimulation was not caused by differences in the visual appearance of the stimuli was confirmed in the second experiment where the monkey was trained to rotate a handle connected to a patterned cylinder in order to generate visual motion stimulation over a fixation point. 61% of the tested cells discriminated between pattern motion generated by the monkey and by the experimenter. It was shown that the monkey's motor activity as such (turning a handle without visible cylinder rotation) did not affect the cells' spontaneous activity. Some indication was received to suggest that the discriminative mechanism is using not only (motor) corollary discharges but also proprioceptive input. These results also gave evidence of the plasticity of discriminative processing in STP for the animal's life-time experiences. Finally, the cells were studied for their responsiveness for image motion resulting from movements of external objects and movements of the animal's body (self-motion). 84% of the cells responded only to visual object-motion and failed to respond to visual motion resulting from animal's self-motion. The experiments also revealed that area STP processes visual motion mostly in observer-relative terms, i.e. in reference to the perceiver itself.

The results provide one explanation for the functional significance of the convergence of several modalities of sensory (and motor) input in the STP. It is suggested that area STP works as a "neural filter" to separate expected sensory consequences resulting from one's own actions from those that originate from the actions of other animals or environmental events.

Keywords: visual motion, self-induced stimulation, self-motion, macaque, superior temporal polysensory area, single-unit

CHAPTER 1

INTRODUCTION

Modern theories of perception emphasize the active nature of perception. Perception is not considered to be an involuntary automatic processing of all incoming sensory *signals* but includes searching and extracting of relevant *information* for the ongoing behavioural tasks. However, because of the limited processing capacity at the certain high levels of the central nervous system, only a fraction of the flux of the sensory stimulation bombarding sense organs can be further processed.

Behaviour in the natural surroundings causes continuous stimulation upon sensory systems as an inevitable consequence of a mere action. The motor acts of a behaving subject produce basically two different sorts of sensory stimulation: proprioceptive and exteroceptive. Proprioceptive stimulation results from the excitation of peripheral sensory receptors, such as muscle spindles, tendon organs, and receptors in the joints, as a consequence of muscle contractions and movement of body parts. Motor acts can lead to innumerable kinds of exteroceptive stimulation affecting multiple sensory systems. Tapping your finger onto the surface of a table causes at the same time visual, auditory, and tactile stimulation in addition to proprioceptive changes.

In some cases self-produced stimulation can be similar to the stimulation produced by completely external sources, but the nervous system must be able to process them differentially. For example, Gibson (1966) has referred to this distinction by emphasizing the difference between obtained and imposed stimulation. The former is caused by the activity of the animal itself. Instead of entering the nervous system through receptors, obtained stimulation "re-enters" it. Imposed

stimulation, on the contrary, is produced by some state of affairs that does not depend on the individual's own action and it "intrudes upon the course of action". The most familiar example is, perhaps, the perception of stable visual world during our eye movements. Even though the retinal image moves across the retina during saccades and tracking eye movements we do not experience a movement of the perceptual environment. The nervous system must, therefore, handle this visual stimulation differently from that when eyes are still and the environment moves. Similar discrimination between self-produced and non-self-produced stimulation can be found in other sensory systems in various animal species. Chapter 2 of this thesis concentrates on describing examples of sensory mechanisms which show discrimination in processing between self-induced signals and signals of completely external origin.

This thesis is concerned with the processing of self-induced visual motion in a multimodal association cortex in the macaque brain. This brain area is known as the superior temporal polysensory area (area STP, Bruce et al., 1981) located in the superior temporal sulcus in the monkey. The main impetus for the experiments described in this thesis came from the findings of Mistlin (1988) and Mistlin and Perrett (1990) who studied somatosensory processing in this area. Their results showed that processing of somatosensory information within area STP was modulated if information about the tactile stimuli were provided through another sensory channel (vision), or if the monkey produced the stimulation itself. The results were discussed in the general context of the effects of *expectation* on the sensory processing in area STP (these studies will be described in detail in sections 2.4, 2.6 and 3.3.3). As area STP, however, is best known for its central role in high-level visual processing, the present study was set up in order to investigate whether processing of visual information might show similar response features. Chapter 3 will provide an overview of the visual processing within the primate visual system and will present the anatomy, connections and functional properties of area STP. As this brain area is a

member of a variety of "processing streams" it is felt essential to give some information about the characteristics of other, functionally related brain areas as well. Chapter 4 binds the two literature review chapters together and presents a rationale for the experimental work to follow. The rest of the thesis presents the experimental work.

CHAPTER 2

PROCESSING OF SELF-INDUCED AND EXPECTED STIMULATION AT THE NEURONAL LEVEL

2.1. INTRODUCTION

This chapter is aimed to search for examples where neurophysiological single-cell recordings have revealed that self-induced sensory input is processed differently to externally-produced stimulation. As the experimental work in this thesis has been carried out by using monkeys as subjects, the literature review concentrates heavily on primate studies. Secondly, this chapter also describes instances where the subject itself has more or less a role of a passive perceiver and the processing of sensory stimulation is influenced by the effects of expectations which are based on previous information delivered to the subject about the nature of the incoming stimulus. The effects of expectation on the processing of incoming sensory signals will be categorized into two broad categories here. In the first case it is possible to observe changes in the neuronal activity *before* any sensory stimulus is received by the sensory system (i.e. as if the nervous system was *anticipating* the stimulus), whereas in the second case the effects of expectation are evident in the differential treatment that expected stimuli and unexpected stimuli receive *after* entering the nervous system. Even though the modulatory effects of self-induction and expectation on the processing of sensory information have been separated for the clarity of presentation, it should be noted that they are closely interlinked phenomena. One is inclined (at least after a certain amount of experience) to form expectations about the (sensory) outcomes of one's own actions. It has also been suggested that expectations about some biologically important stimuli may be hard-wired, for example, reactions to

one's own movements, imprinting and innate reactions to conspecifics, predators and food (Bullock, 1988). In this context it should also be kept in mind that expectations do not have to be conscious states of mind, but can develop and extend their effects on sensory processing automatically.

2.2. SELF-MOTION

Present understanding regards image motion as a fundamental visual dimension with the same status as brightness, depth, size and colour. Movement as a visual quality provides undoubtedly very powerful signals for animals about events of interest or danger in their environment (Bruce & Green, 1990). Detecting the movements of other animals or objects, however, is only one of the several functions that image motion processing serves in vision (Nakayama, 1985). In addition to this most obvious use of motion sensitivity, Nakayama (1985) has listed six very diverse functions for motion processing. According to him image motion processing has a role in a) encoding of the third dimension, b) providing an estimate of the "time to collision", c) distinguishing "figure" from "ground", d) providing information about observer's own movements in relation to environment, e) driving eye movements and f) assisting in pattern vision. The multitude of the functions suggests that there might exist several parallel motion processing systems.

This and the following section focuses on the visual image processing that results from the animal's own action. As described in the introductory section this type of visual motion provides one class of sensory input that can be considered to be expected, and furthermore it provides evidence for the existence of more than one motion processing system. It will be shown that self-locomotion when the body actually moves results in characteristic visual motion cues that are processed differently from those resulting from movements of external objects. In addition,

during self-motion other sensory systems provide the animal with information that is capable in modifying the concomitant visual motion processing.

Object-motion vs. self-motion. It has long been recognized that the visual system must distinguish object-motion characteristics which help define object identity and actions of other animate objects from self-induced visual motion that instead help define the action of the observing organism (von Helmholtz, 1911; von Holst & Mittelstaedt, 1950; Gibson, 1966). In most cases the deformation of the retinal image due to ego-motion is qualitatively different from that caused by object motion. As an observer moves in the world the locomotion will be accompanied by flow in the optic array. The nature of optic flow patterns is specific to certain types of movement (Fig. 2.1). For example, approach is accompanied by centrifugal expanding of the texture elements in the world whereas retreat would be specified by inward streaming of optical texture elements towards the pole of the optic flow field (Bruce & Green, 1990).

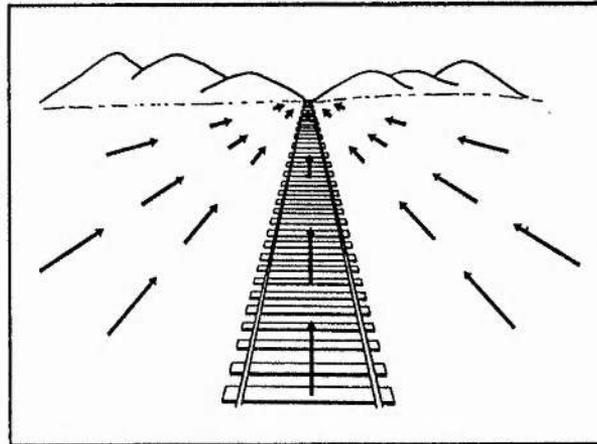


Figure 2.1. An illustration of the optic flow field during retreat. The optical texture elements stream inwards towards the pole of the optic flow field. (From Bruce & Green 1990).

The characteristic nature of optic flow in signaling different types of self-motion led Gibson (1966) to suggest that vision is not only exteroceptive, providing information about events extrinsic to the animal, but also proprioceptive in obtaining

information about an organism's own actions. The importance of the visual stimulation for the sensation of self-motion becomes evident in artificial experimental situations (sometimes occurring in natural conditions as well) where appropriate visual flow stimulation leads to an experience of ego-motion of a stationary perceiver. Visual flow stimulation can override the vestibular, kinesthetic and somatosensory systems of a stationary perceiver and lead to an illusionary sensation of self-motion (Brandt et al., 1977; Dichgans & Brandt, 1978; Berthoz, 1981; Probst et al., 1985). Experiments with large optokinetic drums have revealed that particularly stimulation of the peripheral visual field induces vection (perception of self-movement), even when there is a conflict between the central visual field and the periphery (Brandt et al., 1973). It should be noted that illusionary self-motion can be evoked also by a somatosensory/kinesthetic stimulation in an objectively stationary observer and, like visual stimulation, this can predominate over the vestibular system (Brandt et al., 1977; Bles, 1981; Probst et al., 1985).

The effects of visual flow stimulation have been shown to be powerful enough to be able to trigger compensatory reflex action for maintaining the postural balance (Lee & Aronson, 1974). In fact, the kind of reflexes triggered by typical visual flow patterns may be innate ("time to collision", Nakayama, 1985). Bower et al. (1970) and Ball and Tronick (1971) reported that young babies without experience about the effects of colliding objects exhibit defensive distress reactions (pulling the head backwards and raising arms to cover the face) to "looming" (optically expanding) display images. Similar results have been reported with infant rhesus monkeys (Schiff et al., 1962).

The fundamental reason for the requirement of separate processing between self-motion and object-motion stems probably from the fact that the visual system must be able to detect object-motion relative to an objectively stationary environment in the situation where the perceiving subject is itself moving in the environment.

Under natural, environmental conditions the visual system, however, does not work in isolation or alone, but the sensation of self-motion is induced by multimodal interaction of the visual, the vestibular and the somatosensory systems (Probst et al., 1985). In fact, the role of vision in motion (and self-motion) perception is greatly modified when the observer is not just a passive stationary participant in a laboratory experiment but locomotes actively in the environment (Berthoz, 1981). Even in laboratory conditions the predominance of visual stimulation over vestibular stimulation is not absolute, but the perception of visually induced self-motion can be modulated by simultaneous vestibular stimulation in a passively moved subject (Probst et al., 1985).

Psychophysical experiments with humans have shown that thresholds for the detection of external object motion are elevated under conditions which mimic the stimulation received during natural locomotion and which induce the sensation of self-motion. Probst, Brandt and Degner (1986) studied the effects of induced self-motion on concurrent object-motion detection and found significantly raised thresholds for object-motion detection when self-motion perception was induced by either visual, vestibular or cervico-somatosensory stimulation (by having the subject's head fixed stationary and rotating his trunk). Moreover, it was shown that these different sensory channels mediating self-motion perception had a cumulative inhibitory effect on object-motion perception.

Neurophysiology of self-motion. Self-motion signals from different sensory systems can be combined at various levels of the brain, i.e. vestibular nuclei, cerebellum, thalamus and neocortex. The vestibular nuclei are the focus of convergence of fibres from the visual system and from cutaneous and neck proprioceptors (Berthoz, 1981). Single-units in the macaque vestibular nuclei which respond to stimulation of the horizontal semicircular canals have been shown to exhibit consistent frequency changes when stationary animals are exposed to moving visual fields or when they are

exposed to vestibular-visual stimulation, i.e. rotation in the light (Waespe & Henn, 1977). At the thalamic level where vestibular nuclei send their projections (ventro-posterior nuclei, see Fig. 2.2) pure optokinetic visual stimulation and pure vestibular stimulation often results in comparable responses. By comparison to the vestibular nuclei visual input at the thalamic level produces stronger responses with shorter latencies suggesting a greater visual contribution to visual-vestibular interaction at the higher levels of processing. A proportion of the thalamic units also respond to limb movements (Büttner & Henn, 1976; Büttner & Lang, 1979).

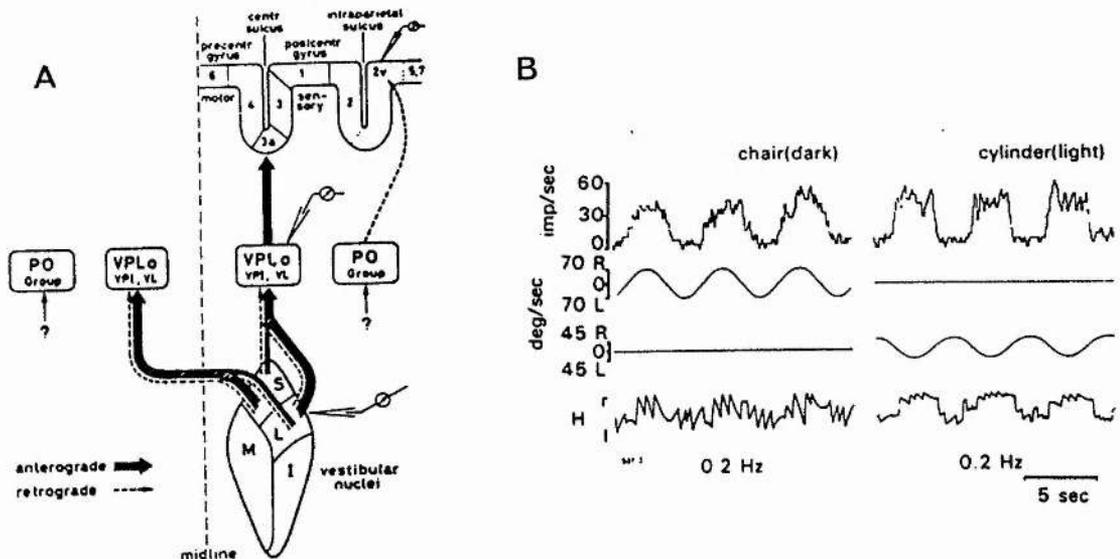


Figure 2.2. A) Diagram of the ascending vestibulo-thalamocortical projections in macaca mulatta. The vestibular nuclei project to the ipsi- and contralateral nucleus ventroposterior lateralis pars oralis (VPL_o) in the thalamus. VPL_o projects to area 3a and the PO group (posterior group) projects to area 2v in the parietal cortex. The origin of vestibular input to the PO group is unknown. B) Running average response (upper trace) of a cortical vestibular neuron (area 2v) during vestibular (left) and whole field visual stimulation (right). Second trace illustrates the velocity of the turntable on which the monkey was located, third trace is the optokinetic cylinder velocity and the fourth trace is horizontal eye position. (From Büttner & Lang, 1979).

At the cortical level the vestibular system has projections to the parietal cortex. Schwartz and Fredrickson (1971) and Büttner and Buettner (1978) have described a vestibular projection area in the anterior parts of the intraparietal sulcus (area 2v) which, contrary to other modality specific primary fields, was not strictly modality specific but was shown to receive convergent visual and somatosensory input. Similarly to the thalamic level, optokinetic visual stimulation is able to produce comparable responses to the pure vestibular stimulation (Fig. 2.2). Joint movements or deep pressure on the skin influenced the same units which respond to vestibular stimulation. For some units the kinesthetic responses required the rotation of more than one joint in a way which occurs naturally during coordinated movements. This somatosensory-vestibular interaction which is already present at the level of vestibular nuclei and thalamus probably plays a central role in mediating the illusory self-motion evoked by somatosensory/kinesthetic stimulation (Brandt et al., 1977; Bles, 1981; Probst et al., 1985). The thalamic ventro-posterior nucleus also projects to area 3a in the bottom of the central sulcus (Büttner & Lang, 1979). A further area receiving vestibular input and having response properties similar to area 2v has been identified in the upper bank of the lateral sulcus, area PIVC (parieto-insular vestibular cortex, Grüsser et al., 1990a,b). More posteriorly in areas 7a and 7b of the parietal cortex vestibular input has been shown to converge with visual or visuo-motor input (Pause & Schreier, 1980; Kawano et al., 1984). Some of the units recorded in these studies might have been localized in area MST in the superior temporal sulcus (Fig. 1. in Kawano et al., 1984). In fact, Thier and Erickson (1992) have shown that cells in the lateral part of area MST (MSTl) do receive a head-movement related non-visual input which probably originates from the vestibular organs.

The type of visual stimulation (i.e. whole-field movement) which leads to the sensation of self-motion and which integrates with other modalities signalling from self-motion has been shown to be processed separately from visual input originating

from object-motion. Neurophysiological studies from the motion processing systems have revealed neurons which are activated preferentially by whole field movements and neurons which need the motion to be restricted to a part of the cell's receptive field. Neurons in the optic tectum of birds (Frost et al., 1990), suprasylvian area of cats (von Grünau & Frost, 1983), the superior colliculus (Bender & Davidson, 1966) and areas MT and MSTv (Allman et al., 1985; Saito et al., 1986; Tanaka et al., 1986; Sugita et al., 1990) of monkeys have a receptive field organization which consists of two (figure-background) directionally specific mechanisms having opposite directional preferences (see Fig. 2.3). The cells exhibit responses to a local stimulus movement in

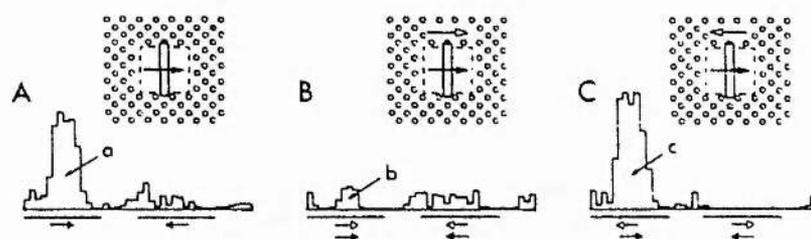


Figure 2.3. Response properties of a MT neuron. The cell responds to a bar movement against a stationary dot pattern (A). Response to the bar movement is suppressed when the dots move in the same direction with the bar (B), but is facilitated when the dot pattern moves in the opposite direction (C). Filled arrows: direction of the bar movement; open arrows: direction of the dot pattern movement. (From Tanaka et al., 1986).

a preferred direction against a stationary background. The responses are facilitated if the background is moved simultaneously in the opposite direction of motion but if the background is moved in phase in the same direction and speed with the local stimulus the responses are inhibited. Such neurons would be particularly sensitive for "real" object-motion relative to the environment and less sensitive for visual motion resulting from ego-motion. It should be noted, however, that self-locomotion in a three-dimensional environment evokes motion parallax and differential motion cues which are likely to activate these neurons as well. (This is easy to demonstrate, for

example, by looking at one's objectively stationary hand against a background at different distances while moving the head sideways. The hand and the background seem to move in opposite directions. In fact, one easily experiences an illusory movement of the hand despite the somatosensory system signals that this is not the case).

In the same way that mechanisms specialized for object-motion detection exist at several neural levels, systems for whole-field movement analysis can be found from various levels as well. Recently neurophysiological experiments have provided evidence that the accessory optic system is a very likely candidate for processing especially this type of visual motion information (Simpson, 1984; Soodak & Simpson, 1988; Frost et al., 1990). Cells in the accessory optic system do not have any inhibitory surround but they are driven best by the movement of large textured patterns at relatively slow speeds. The accessory optic system (AOS) exists in all vertebrates (Fite, 1985) and in most mammalian species (see Fig. 2.4). In most mammalian species the accessory optic system consists of three bilaterally paired nuclei, medial, lateral and dorsal terminal nuclei, that are located at the junction of the midbrain with the diencephalon and that receive a direct retinal projection (Soodak & Simpson, 1988). Comprehensive neurophysiological studies have been carried out on the AOS of the rabbit, cat and birds (see, Frost et al., 1990). The AOS is involved in routing the visual signals to the vestibular systems through several pathways, but the AOS cells do not respond to vestibular stimulation alone. During self-motion and visual whole-field stimulation they show equivalent response properties. It has been suggested that as the visual AOS neurons are specially sensitive for slow velocity motion this property makes AOS as an ideal complement to the vestibular semicircular canal system which is relatively ineffective speed detector for low frequencies of angular head movement (Soodak & Simpson, 1988). Furthermore, when the animals have been subjected to whole field optical rotation along selected axes it has been shown that there are essentially three axes to encode this whole field

rotation. The directions of these axes coincide with the best-response axes of the semicircular canals showing thus that the visual motion detection system at this level shares the same set of co-ordinate axes (Simpson et al., 1988). The response properties of primate AOS neurons seem to differ of those observed in rabbit, cat and birds in that the responses are also evoked by small single objects (Westheimer & Blair, 1974, Hoffmann & Distler, 1989). Hoffman and Distler (1989) have suggested that this is due to the strong projections from cortical areas specialized in motion analysis to the AOS.

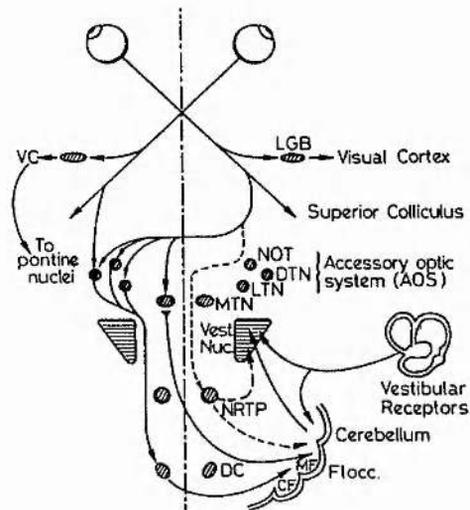


Figure 2.4. Visual pathways to the accessory optic system (AOS) in brainstem. From the retinae visual information is distributed directly to LGB, to pontine nuclei, to superior colliculi and to AOS. The pontine nuclei link with the vestibular system (not indicated). Abbreviations: LGB, lateral geniculate body; NOT, nucleus of the optic track; DTN, dorsal terminal nucleus; MTN, medial terminal nucleus; LTN, lateral terminal nucleus; NRTP, nucleus reticularis tegmenti ponti. (From Berthoz, 1981).

At the cortical level the dorsal part of area MST (MSTd) in primates has been shown to contain cell populations with response properties suggesting a functional role in visual self-motion detection (Tanaka et al., 1986; Saito et al., 1986; Hikosaka et al., 1988; Duffy & Wurtz, 1991a,b). One type of population consists of cells responsive to a straight movement in the frontoparallel plane with unidirectional selectivity. The second class includes cells responding to an expanding or contracting size change of patterns. The third class of cells has two subgroups: cells responsive to a unidirectional rotation of patterns either in frontoparallel plane or in depth (see Fig.

2.5). Like neurons in the AOS, a large fraction of the MSTd cells within each category prefers the movement of a wide field to movement of a small object. It has been suggested that the cells in MSTd are involved, therefore, in the analysis of visual field flow caused by self-movement of the animal. The cells belonging to the first group analyze straight and parallel visual flow caused mainly by eye-movement or head rotation and head, cells in the second group analyze radial flow caused by locomotion, and cells in the third group analyze visual rotational flow accompanied by head bending (Saito et al., 1986; Tanaka et al., 1986; Saito, 1992).

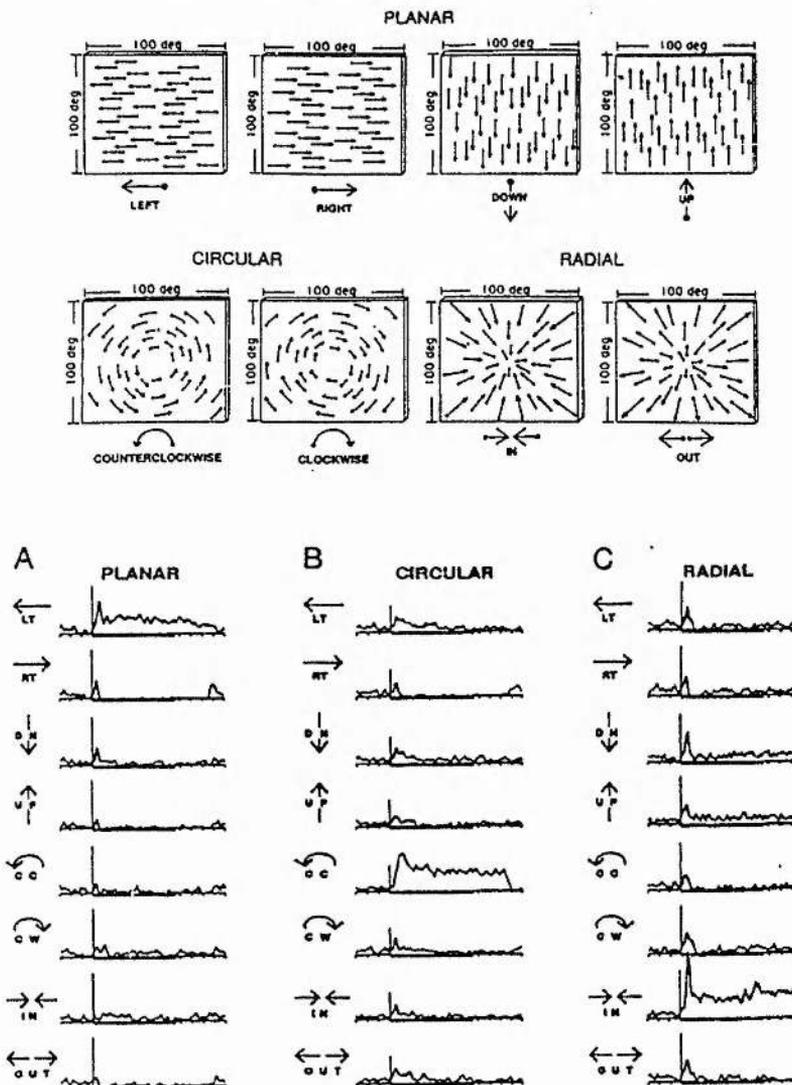


Figure 2.5. Examples of neurons (lower part) that respond to a particular planar, circular or radial whole field flow stimulation (upper part). (From Duffy & Wurtz, 1991a).

Roy and Wurtz (1990) have found that MST neurons that are responsive to motion in the fronto-parallel plane code the direction of movement as well as the depth of motion from disparity cues. When stimulated with random dot displays the neurons responded, for example, when the "foreground" (i.e. in front of the plane of fixation) moved to the left or when the "background" (a stimulus behind the plane of fixation) moved to the right, or both of these movements. Roy and Wurtz argue that even more effective in signalling the direction of self-motion were cells (40% of those tested) which preferred one direction of motion with visual stimuli of one sign of disparity and the opposite direction of motion for stimuli of the opposite sign of disparity. Such a neuron could respond, for example, when the foreground moves to the left or when the background moves to the right or both. This arrangement of optic flow occurs in the situations where the line of sight and the direction of motion are not parallel, for example, during lateral displacement of the head. The proposition that these neurons contribute a signal about the direction of self-motion was further supported by the findings that a predominance of the disparity-dependent direction-selective neurons preferred horizontal motion as opposed to oblique or vertical motion. Macaque monkeys are primarily terrestrial animals and their locomotion occurs mainly in the horizontal plane.

2.3. VISUAL STABILITY DURING SELF-INDUCED EYE MOVEMENTS

The previous section described how visual flow stimulation which usually accompanies self-motion is capable in evoking an illusionary sensation of self-motion in a stationary subject. The special feature of this type of retinal motion stimulation is that it involves rigid displacement of the whole retinal image, a type of stimulus which rarely occurs in natural objective movement. Apart from whole field visual stimulation during body locomotion, such displacements of the retinal image occur almost continuously during our exploratory eye movements. This retinal motion,

however, does not evoke sensation of visual movement (or illusionary self-movement).

Theories accounting for experienced perceptions. When the eye is voluntarily moved and the optical image slips across the retina, we do not experience any movement and the world appears stationary. Instead, a gentle pressure onto the eye-ball leading to a slight lateral displacement of the eye evokes an apparent motion of the visual world (see Fig. 2.6). Experiments with visual afterimages have shown that afterimages (i.e. images with fixed retinal location) appear to move during normal eye movements or with attempts to move a paralyzed eye, but remain still during movements imposed externally onto the eye ball (for a review see Grüsser, 1986). These results have

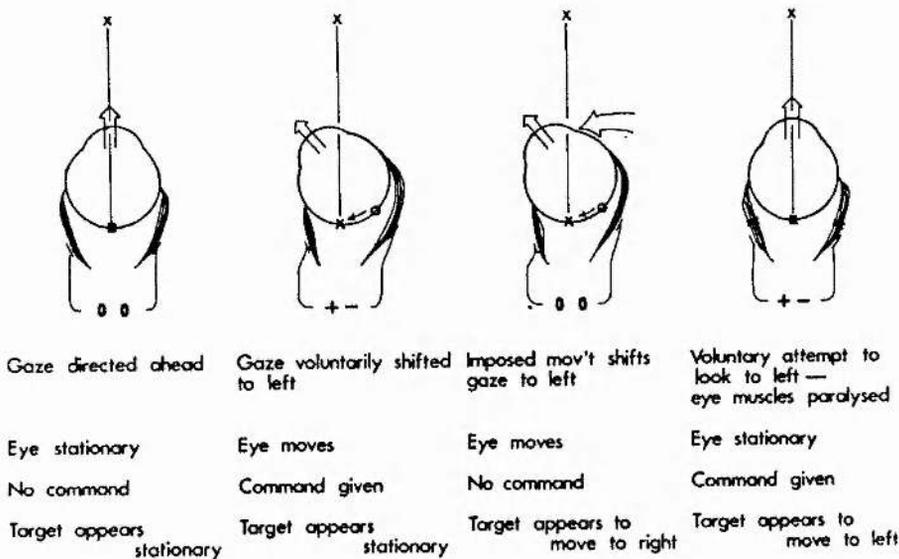


Figure 2.6. Diagrams showing actual positions of the eye, viewed target and its retinal image. Explanations underneath each picture describe the details. Plus (+) and minus (-) signs in the pictures refer only to the agonist/antagonist eye muscle activation. (From McCloskey, 1981).

suggested that information about eye movements must be compared with sensory information about retinal image movement and that there exists some sort of a cancellation mechanism. Afferent visual movement signals during normal eye movements are cancelled by simultaneous efferent command signals generated for the shift of gaze. When the eye-ball is pressed, there are no efferent signals present to

cancel the visual motion signal and this leads to the sensation of visual motion in the opposite direction. Correspondingly, voluntary eye-movement does not result in the retinal displacement of an afterimage and as there is no afferent motion signal present to be cancelled, the subject experiences an illusory sensation of movement of the afterimage.

Sperry (1950) and von Holst and Mittelstaedt (1950) have provided two well known theories of the neural basis of the visual stability during voluntary eye movements. Sperry (1950) introduced a notion that the motor command centers generate two types of signals: a *motor command* to oculomotor centers for moving the eyes and a *corollary discharge* into the visual centers to compensate for the "expected" retinal displacement. Von Holst and Mittelstaedt (1950) presented a slightly different theory in which they proposed the motor command to be accompanied by an *efference copy* to the sensory systems. An efference copy is sent to sensory structures simultaneously with a command sent from the oculomotor structures to move the eyes. This efference copy can be supposed to be a positive (+) signal whereas the sensory signal ("re-afference") caused by eye movement is a negative (-) signal. When these two signals are summed at some level in the central nervous system, no signal of movement arises and the visual surround is perceived as stable (Fig. 2.7).

The efference copy-reafference system sets very demanding requirements to the neural systems in translating one or both neural signals into comparable format for carrying out the subtractive computations. MacKay (1973) has proposed a role for corollary discharges which is less demanding than in the efference copy theory. The sensory changes due to voluntary movements need not be eliminated from the sensory input, but need only be appropriately evaluated. According to MacKay perceivers build up an internal representation ("a map") from their environment which is stored and expected to be invariant. Changes in sensory input caused by voluntary

movements would not contribute any information about the environment itself and, therefore, would not modify the representation. In this model, there would be no question of suppressing these reafferent sensory signals as they would be used for

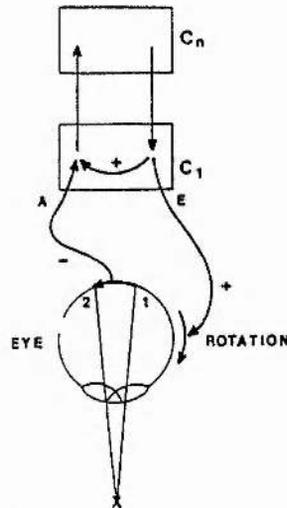


Figure 2.7. The efference copy - re-afference principle. An efferent command is sent from a motor center (C_1) to move the eye to the right. An efference copy of this signal marked with a plus (+) sign is also sent to a sensory center. This sensory center receives an afferent sensory signal from the retina which indicates that the point x on the retina has moved from 1 to 2. This afference (re-afference) has a minus (-) sign and it is cancelled by the efference copy (+ signal). Higher centers (C_n) receive no message of motion. (From Hyvärinen, 1982).

providing sensory feedback for the guidance of the locomotor activity. The function of corollary discharges is to provide information (or set criteria) to the central mechanisms to evaluate whether incoming afferent sensory signals require a readjustment of the internal representation of the environment.

Observations about apparent movements of the visual world caused by external force on the eye ball, or similar sensations in patients with *weakened* eye movements, seem to exclude the possibility of extraocular kinaesthetic signals having any effect on visual perception. The "outflow" theory of motor signals to sensory brain areas as a cancellation mechanism has, however, been challenged by an "inflow" theory advocating that proprioceptive information from the extraocular muscles and other orbital structures is responsible for maintaining the perceptual stability by interacting with the afferent visual movement signals (James, 1890;

Sherrington, 1918). It has been shown that normal subjects with *completely paralyzed* eye muscles by drugs do not experience displacement of the visual world on attempting to move their eyes (Siebeck, 1954; Brindley et al., 1976). Brindley et al. (1976) also studied the effects of drug induced paralysis of one eye on movements of retinal afterimages. Afterimages formed in the completely paralyzed eye did not move during attempts to move the eyes, whereas this illusion was perceived in the other, non-paralyzed eye. At least a part of these differences between the studies just described and the early studies may be explained by the fact that in the early studies the patients' eye muscle paralysis was not complete (Brindley et al., 1976; McCloskey, 1981). Referring to the possible role of afferent proprioceptive information from eye muscles in visual stabilization during eye movements, McCloskey (1981) points out that afferent input may be more effective during voluntary eye movements as compared to imposed rotations. "The mechanical state of the extraocular muscles, the background of contraction-induced proprioceptive reafference, and the central neural context into which afferent impulses flow could all be expected to be different in active and imposed eye movements." McCloskey considers the possibility that corollary discharge acts as a gate allowing relevant kinaesthetic input access to perceptual mechanisms only during self-induced, voluntary eye movements. Thus during normal eye movements "expected" self-initiated retinal motion would be ignored by central mechanisms on the basis of incoming proprioceptive input and an efference copy of command signals.

The experimental results described so far have usually been taken to show that retinal signals can not play any role in mediating visual stabilization during self-induced eye movements. Gibson (1966) by contrast has advanced theories that the displacement of the whole retinal image is a signal which could be used for visual stabilization during self-induced eye movements. It should be noted that voluntary eye movements consist of fast saccadic eye movements separated by periods of fixation. The saccadic velocities are much higher as compared to velocities produced

by pressing the eye ball. For example, the peak velocity of a 20 degree saccadic eye movement reaches 900 degrees/s (Wurtz et al., 1980). Smooth pursuit eye movements, such as those in tracking a moving target or those generated by vestibular stimulation, are evoked reflexly and are much slower. Their function is to stabilize the retinal image of a target when either the target or the head moves. Saccadic eye movements differ from slow pursuit movements in several perceptual and physiological characteristics and they are generated by two different oculomotor sub-systems (Leigh & Zee, 1983). It is possible that the lack of voluntary control over smooth pursuit movements is a naturally evolved mechanism to prevent an illusory sensation of "world motion". Interestingly, if a slowly moving object is tracked with a smooth pursuit movement, subjects tend to experience a illusory motion of the background (i.e. the whole field). This is known as the Filehne illusion (Filehne, 1922; Mack & Hermann, 1973). In this case the motion sensation is, however, complicated by other motion cues present (i.e. relative movement between the target and background). A smooth pursuit in absence of a target would produce an optimal experimental situation for comparing slow velocity image movement caused by real object motion with that caused by eye motion. Unfortunately, as mentioned above, voluntary pursuit in the absence of a target is impossible.

MacKay (1970) presented an idea that the sweep of the whole visual world across the retina during a saccade may result in "something of an insult to the dynamic balance of the visual nervous system". He obtained evidence in favour of his hypotheses from experiments in which the eye itself was held stationary, but the visual field was displaced in a saccadic fashion. However, he remarked that although in some cases the suppressive effect in vision during a saccade can be explained without any need for inhibitory corollary discharges, this kind of mechanism may operate as well, together with the whole field retinal displacement suppressive mechanism. This view has been supported by Stark and Bridgeman (1983) who proposed that in a normal structured environment retinal signals override influences

of corollary signals. Corollary discharges provide the information about eye position in darkness, and they have a role especially in intersensory coordination of vision with other modalities in both structured and unstructured visual conditions.

Stevens et al. (1976) presents a theory for the existence of three independent systems in explaining visual stabilization which also accounts for some of the controversies in experimental results. They studied visual perceptions during drug-induced paralyzes. One of the crucial findings was that attempts to make saccades during partial paralysis resulted not in the sensation of dynamic motion of the visual field (as earlier studies had described) but a sudden "static displacement" of the field, i.e. a jump of the field from one position to a second. According to their theory an *eye position system* receives input from sensory receptors located in the conjunctival sac and extraocular muscles, and this system is responsible for the sensation of effort reported by their subjects during attempted eye movements. A second *pattern visual system* receives its input from the retina. When the whole retinal surface is activated by a large rapid image movement (e.g. during a saccade), pattern vision is suppressed, whereas an activation of a limited area of retina by an image movement leads to perception of movement. This way the pattern system may distinguish between self-induced image movements and movements of objects in the external world. Finally, Stevens et al. (1976) propose a *spatial system* which is responsible for perceptions of spatial localization receiving an input from the retina and a corollary discharge from motor centres. This system makes it possible to differentiate between self-induced displacements and external displacements of visual world, producing a perceptually stable visual world.

Neurophysiological studies. Now, it seems to be a fair assumption that in the visual system there should be neural elements whose activity is related, not to the movement across the receptive field on the retina per se, but to the real movement of objects in

the visual field, independently of the eye movements, and indeed, this type of neuron has been found in several visual areas.

Single cells in monkey's superior colliculus have been found to respond selectively to real stimulus movement and to "ignore" comparable motion of stimuli across the retina produced by saccadic eye movements (Fig. 2.8; Robinson & Wurtz, 1976; Richmond & Wurtz, 1980). Moreover, these experiments showed that the

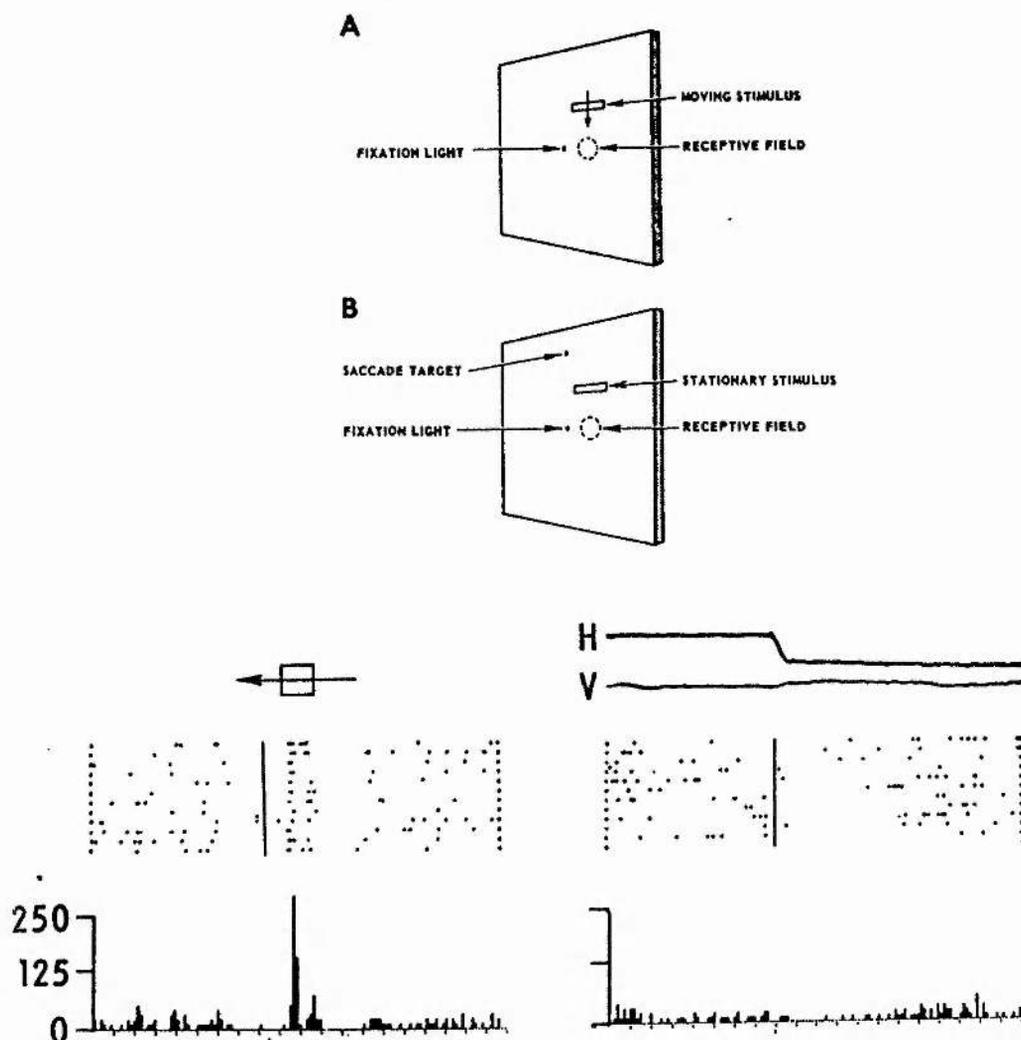


Figure 2.8. Upper: Schematic representation of the (A) stimulus movement across a stationary receptive field and (B) eye movement causing the receptive field to sweep over a stationary stimulus. Lower: Response of a cell recorded from superior colliculus to stimulus movement in front of the stationary eye compared to the response to eye movement across the same stationary stimulus. The stimulus velocity across the receptive field matches that of the horizontal (H) saccadic eye movement (900 degrees/s). (From Robinson & Wurtz, 1976).

discrimination is caused by an extraretinal signal suppressing the visual responses in collicular cells (evident from the suppression of spontaneous activity in the dark during eye movements), and that the most likely source of this extraretinal input is a corollary discharge from some part of the oculomotor system. Similar results have been obtained from the pulvinar which receives a direct projection from the superior colliculus (Robinson & Petersen, 1992). Even though the existence of connections from oculomotor muscle spindles to the superior colliculus has been demonstrated (e.g. Cooper & Fillenz, 1955), the possibility of this suppressive input being of proprioceptive origin has been excluded. For example, the latency of the suppressive input acting on these collicular cells was too short to originate from oculomotor muscle spindles (Robinson & Wurtz, 1976), and the suppression persisted even after blocking of motor and proprioceptive nerve fibers entering and leaving the orbit (Richmond & Wurtz, 1980).

Evidence in favour of corollary discharges providing eye position information in monkeys has also been reported by Guthrie et al. (1983). They showed that monkeys with transections of the ophthalmic nerves (which eliminated extraocular muscle proprioception) were able to generate accurate compensatory saccades after perturbation of eye position produced by stimulation of the superior colliculus, to targets which were extinguished before the eye position perturbation.

The inhibitory effects at the collicular level during saccades are not, however, only extraretinal in origin. Wurtz et al. (1980) have shown that many cells in the superior colliculus exhibit attenuated responses during saccades simply because of the inhibitory effects resulting in visual stimulation of the surround of the cell's receptive field when the image is swept across the retina (Fig. 2.9). These retinal mechanisms do not differentiate whether the retinal sweep results in animal's own saccadic eye movement or external movement. The existence of two overlapping mechanisms, a corollary discharge and retinal surround suppression mechanism, ensures the

effectiveness of the visual stabilization in a wide variety of conditions. The corollary discharge mechanisms are effective over a wide range of light and contrast levels, but modify the responses of only a half of the collicular cells. The retinal mechanisms instead affect all cells but work reliably only in a patterned visual environment with high contrast levels present.

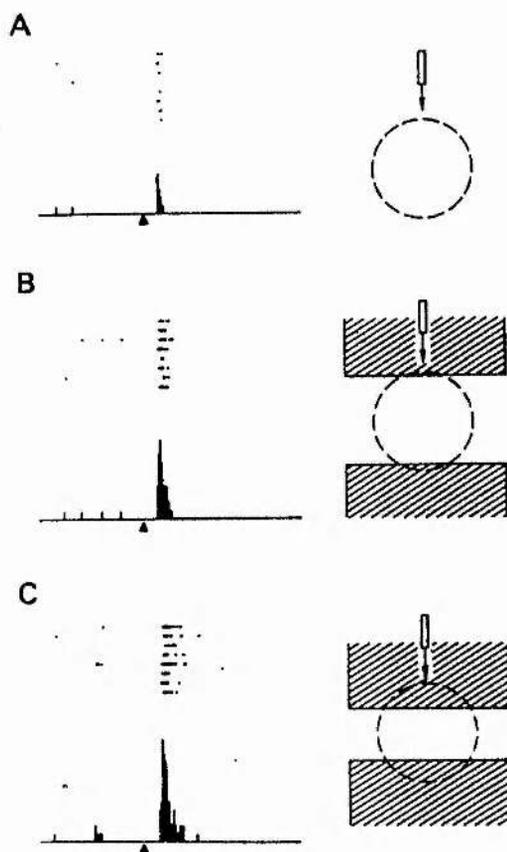


Figure 2.9. Response of a collicular cell to stimuli moving across the cell's receptive field (dashed circle). **A)** Response of the cell to a stimulus which moves across the suppressive surround of the cell before entering the receptive field. **B)** and **C)** The responses were improved when the surrounding areas of the receptive field were shielded. The approximate time at which the stimulus crossed the receptive field is indicated by the arrow beneath each histogram. (From Wurtz et al., 1980).

Frontal eye fields have been suggested as a likely source of the extraretinal suppressive input to the superior colliculus (e.g. Robinson & Wurtz, 1976). Bizzi (1968) and Bizzi and Schiller (1970) recorded units from the monkey's frontal eye fields during saccadic and smooth pursuit eye movements. Frontal eye field cells

received neither proprioceptive or visual information. The activity of one type of the cells was correlated solely to the motor component during saccades, whereas the second type of cells was found to code eye position. The finding that the activity of both cell types began *after* eye movements indicated that these cells were not involved in creating eye movement commands, but were very suitable for producing corollary discharges to other brain areas. However, monkeys with ablations of the frontal eye fields still show suppressive activity in the superior colliculus, which makes it questionable that the frontal eye fields are the (only) source of corollary discharge (Richmond & Wurtz, 1980).

While the above results indicate that saccades affect the processing of visual information in the tectopulvinar visual system, the geniculocortical pathway at the level of lateral geniculate nucleus remains visually sensitive during saccades and no visual and oculomotor interaction has been observed in LGN cells (Büttner & Fuchs, 1973).

First attempts to find differences similar to those observed in the superior colliculus in cortical visual neurons turned out to be not very successful. Wurtz (1969) compared responses of V1 neurons in the monkey cortex during stimulus motion resulting from saccadic eye movements and motion of external stimuli with a comparable speed. The general finding was that while all the recorded neurons gave excitatory responses to stationary stimuli, responses to real stimulus motion or stimulus motion caused by eye movements were more variable and weaker, and that if the cells responded, there were no differences in responses between these two conditions. The lack of response discrimination can be explained, however, by the effects of inhibitory surround like those of collicular cells (Judge et al., 1980). Moreover, as Judge et al. (1980) have pointed out, if there was a clear extraretinal input to the striate cortex suppressing the visual input during saccades, such a

suppression might be evident perceptually as a pause in continuous vision. This is not our experience.

When comparisons have been made between responses to slow stimulus movements and to equivalent stimulus conditions during tracking eye movements, striate cells have also been observed to differentiate between these two conditions. Fischer et al. (1981) reported stronger responses to slow real stimulus movement in about 5% of the recorded striate neurons (from their Fig. 5). Galletti et al. (1984) have reported 10% of the cells in V1 to be sensitive only for "real motion" (i.e. stimulus motion across stationary retina).

In the prestriate visual areas the proportion of cells discriminating between self-produced and externally-produced motion across retina is considerably higher. The general rule seems to be that the proportion of such cells increases as one records from visual areas increasingly higher in the hierarchy of visual areas. In area V2, Galletti et al. (1988) reported about 14% of the studied neurons gave high responses to real moving stimuli, but weak responses to equivalent retinal image displacements due to eye movements. In area V3a the proportion of these 'real-motion' cells has increased to 48% (Galletti et al., 1990).

These results, however, have been recently criticised by Erickson and Thier (1991). They recorded forwards along the visual pathway starting from area V1 to areas MT and MST and found that all the cells up to the level of area V4 and almost all the cells in area MT responded indiscriminately to retinal motion arising from externally-induced stimulus motion and motion resulting from animal's own eye-movements. By contrast, almost all cells in the dorsal area of MST (MSTd) as well as a small proportion in ventral MST were found to discriminate between these two types of retinal motion. They concluded that "discrimination of self-induced visual motion is common only in some extra-striate areas and that the incidence of this

property increases within the STS along a posterior-to-anterior axis from MT to MST" (Erickson & Thier, 1991).

The difference in results from those of Galletti and his co-workers could be, not necessarily due to shortcomings in controlling experimental variables as suggested by Erickson and Thier (1991), but rather because of the backward projections from area MST to cortical areas at the earlier stages (see Fig. 3.2 in Chapter 3 and for a review of the cortical connectivity see, Felleman & Van Essen, 1991). If it is postulated that area MSTd presents the stage in the hierarchy of visual motion analysis which is responsible for processing self-induced retinal motion input differently from externally-induced signals, MSTd could return the discriminated information to lower levels. It is not surprising that Erickson and Thier (1991) did not find real-motion or 'passive-only' cells from area V4. This would be because there does not exist a projection from area MSTd back to area V4, whereas MSTd does project directly back to areas such as MT, V3A and V2, and real-motion cells in V1 would in turn depend on influence of back projections from V2 to V1. When it comes to areas below V4, it is not clear exactly which areas Erickson and Thier (1991) recorded from, and in any case the number of the recorded cells was so small (as the total number of cells recorded from V1-V4 was reported to be 24) that it is hardly surprising that they did not find any passive-only (real-motion) cells from these areas. According to Galletti et al. (1984, 1988, 1990) the proportion of real-motion cells was 10%, 14% and 41% in areas V1, V2 and V3A, respectively.

At the cortical level the visual stabilization during pursuit results from both extraretinal and retinal mechanisms. Data obtained with uniform visual background in darkness and against textured background indicates that real motion cells receive either retinal or extraretinal inputs, or in some cases both type of eye motion input (Galletti et al., 1984, 1988, 1990). In most cases the spontaneous activity of the neurons receiving only an extraretinal signal is not affected by tracking movements

alone (Fig. 2.10). This suggests that where the corollary discharge is acting its input selectively inhibits the visual input but does not induce a general shut down of responsiveness. In this respect there is an important difference in comparison to the processing in the superior colliculus. Collicular cells do show a general suppression of spontaneous activity connected to the saccadic eye movements themselves, instead of a selective inhibition of visual responses (Robinson & Wurtz, 1976; Richmond &

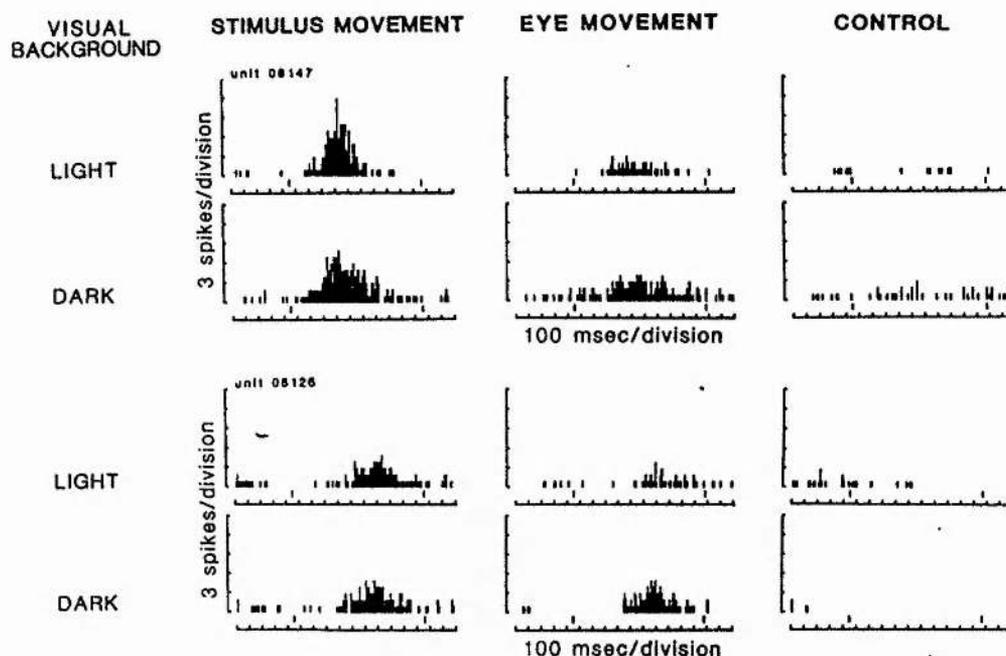


Figure 2.10. Responses of two "real-motion" cells during stimulus movement (steady fixation), during tracking eye movement and during tracking eye movement without any visual stimulation on the receptive field (control). The cell above maintained its real-motion behaviour also when tested with an illuminated stimulus in darkness. This indicated that the cell received an extra-retinal input. The cell below failed to show real motion behaviour in darkness which suggest that this cell received a retinal signal. (From Galletti et al., 1990).

Wurtz, 1980). Cells in areas MT and MSTv, as described in the previous section, also contribute in generating the retinal stabilization mechanisms through the surround suppression of large field motion (Allman et al., 1985; Saito et al., 1986; Tanaka et al., 1986; Sugita et al., 1990).

Single unit recordings from the posterior parietal cortex have revealed response properties that seem to provide physiological support for the theories of

MacKay (1973) which were described earlier. He proposed that corollary discharges are not used to eliminate the sensory changes due to voluntary eye movements but to provide information to the central mechanisms that the internal representations perceivers have build up and stored from their environment do not need readjustment. Recently, Duhamel et al. (1992) have shown that for some parietal neurons the location of the receptive field shifts transiently in accordance with the intended eye movement before the eye movement is actually executed. This shows that parietal neurons 'anticipate' the retinal consequences of intended eye movements. Moreover, those parietal neurons which do not show predictive remapping do exhibit, however, responses that reflect a visual memory trace that has been remapped in conjunction with the eye movement. These neurons respond when the eye movement brings the stimulus into the receptive field, even though the stimulus has been distinguished earlier. Duhamel et al. (1992) suggest that these response properties reflect the effects of signals corollary to eye movements and that they cause the parietal representation of the visual world to undergo a shift that predicts the location of reafferent visual input.

In summary, neurophysiological studies have shown that the most widely studied structures, superior colliculus and cortical visual areas receive a corollary discharge type of input from motor centres suppressing or inhibiting visual responses during eye movements. The corollary discharges assist in the discrimination between retinal motion that arises as a result from one's own eye movements and retinal motion caused by movements of external objects. This discriminative function is supported by a second group of mechanisms because the same brain areas also contain cells which differentiate between movements of the whole visual field (usually caused by eye movements) and object movements which are restricted in a part of the visual field. Combined with psychophysical studies in humans it seems highly probable that both mechanisms are used by the visual system for stabilizing visual perceptions during self-induced eye movements. The functional difference

between the two mechanisms could be that corollary discharges facilitate the detection of real movement in the environment over a wide range of light and contrast levels, and provide information about spatial attributes of the environment to other sensory systems, whereas processing of whole field motion and selective sensitivity to local relative motion provide highly accurate information of movement in the complex, illuminated visual world. Two parallel systems secure efficient function over a wide range of external conditions.

2.4. PROCESSING OF SOMATOSENSORY STIMULI AS A RESULT OF ACTIVE EXPLORATORY MOVEMENTS

As Gibson (1966) points out "the perceptual capacity of the hand goes unrecognized because we usually attend more to its motor capacity, and also because the visual input dominates the haptic in awareness". Indeed, it is interesting to compare exploratory hand movements and exploration of the visual surroundings with voluntary eye movements. A quick comparison would show that both "perceptual systems" consist of a movable organ having a mosaic of sensory receptors (skin/retina) attached to it.

Despite the apparent similarities, there are some important differences as well. As was described above, during exploratory eye movements (i.e. saccades) the visual system becomes more or less insensitive, not only to the retinal motion stimulation, but to all visual stimuli, and hence visual information is mainly gathered only during fixation periods. The hand/tactile system, instead, is not only sensitive to shape and texture when the skin is resting stationary relative to the perceived surface, but it is generally accepted that sensory discrimination performed by active hand or finger movements is superior to passive discrimination (McCloskey, 1981). In fact, Gibson (1962) regarded these active and passive conditions to stimulate separate perceptual

subsystems. He remarked how sensory psychology had failed to emphasize the difference between active touch (touching) and passive touch (being touched). Active touch is purposive by its nature and it consists of two kinds of input information, objective and subjective. What is most important, the purpose of active, exploratory hand movements is to isolate and enhance objective components over the subjective ones.

Single-unit recordings from the somatosensory cortex (areas 1 and 2) in monkeys have revealed tactile neurons which are closely related to active exploratory hand movements (Iwamura et al., 1985). The cells exhibit stronger responses when the tactile stimulation results from active touch as opposed to otherwise similar, but passive tactile contact. Both excitatory and inhibitory activity changes are present. Some neurons signal the movement of skin relative to the object, and again for these cells active hand movement over the surface texture produces stronger responses as compared to object motion across a passive hand/skin. The receptive fields of the cells have very precise requirements and, for example, an activation may necessitate an active manipulation of an object with two particular fingers. What is especially interesting, is that the cell discharges do not precede the contact of finger with the objects (cf. the response properties of posterior parietal neurons which are described later).

Somewhat surprisingly, perhaps, Dyhre-Poulsen (1978) has reported attenuated responses in the medial lemniscus in monkey to electrical and tactile stimuli before and during a lever-pressing movement made by the limb receiving the stimulus. Psychophysical experiments have revealed elevated thresholds to vibratory stimuli applied to human fingers performing ballistic and tracking movements (Dyhre-Poulsen, 1978). Similar results have been reported by Coquery (1978) who observed perceptual suppression to brief electrical stimuli applied to a fingertip during flexion of the same finger. He studied two alternative mechanisms for explaining

these results; afferent suppression induced by displacement of the stimulated skin area, or inhibition by descending motor commands. Psychophysical experiments showed that the perceptual suppression started more than 100 ms before the onset of muscular activity, but similar perceptual attenuation was also observed before and after a passive displacement of the stimulated skin area. These results were taken to suggest that active or passive displacement of the stimulated skin area may cause inhibition of afferent somatosensory input transmission and induce perceptual masking. In this respect all these results resemble those obtained with saccadic eye movements as described in the previous section. It was argued that saccadic suppression involves both motor (corollary discharge) and afferent (retinal displacement) mechanisms.

The results described above seem to contradict the notion that active movements of the hand enhance its capacities in perceptual tasks. One reason for this seeming discrepancy could be that the simple movements that the subjects were required to perform during the experiments were not of an exploratory character, controlled by tactile and proprioceptive feedback (Gordon, 1978). Another possibility is that observations of overall reduction of ascending activity as made in macroelectrode recordings at different neural levels may conceal a pattern of selective depression. For example, in exploratory movements the spatial acuity might be improved by increasing lateral inhibition in a relay nucleus, but a macroelectrode recording would only show a general attenuation of activity (Gordon, 1978).

At the higher cortical stages of somatosensory processing Mistlin (1988) and Mistlin and Perrett (1990) have shown that single-unit responses in the macaque temporal cortex could be modulated in some instances by the degree to which the monkey could expect the occurrence and nature of tactile stimulation. When the monkey's active exploration leads it to encounter repeatedly an object of a particular texture and compliance at a particular location, the object's tactile properties can be

said to become "expected". Active exploratory hand movements made out of sight by the animal itself were found to produce no tactile responses when the monkey contacted familiar, expected surfaces such as its own body or highly familiar items within reach. By contrast equivalent tactile stimulation as a result of encountering novel, unexpected surfaces produced vigorous neuronal responses. What kind of information is then used for forming expectations about one's incoming tactile sensations? The authors suggested that this requires knowledge of the tactile surface properties of the objects in the environment, spatial memory for the normal location of objects in the environment and information as to the current position and trajectory of limb movements. In fact, visual information could have been added to the previous list, but as it reflects the effects of intersensory information transfer, this case is handled separately in section 2.7.

2.5. ATTENUATION OF RESPONSES TO SELF-VOCALIZED SOUNDS

Most vertebrates rely on vision in orienting their behaviour with respect to the environment, and it is the visual system which provides the information necessary for responding adequately to such environmental features as size, shape, distance, nature and movements of objects (Henson, 1965). However, some of these functions are shared by the auditory system. In humans it is easily forgotten that audition, besides its social-communicative role, can play an important role in assessing the nature and movement of animate and inanimate objects. Experiments with blind people have shown that the human ear is capable to make relatively fine size discrimination, simple shape discrimination, and target location in space based on echo-information received from self-emitted vocal sounds (Rice & Feinstein, 1965; Rice, 1967).

Müller-Preuss (1983, 1986) has investigated the response properties of various stations in the auditory pathway during vocal activity in squirrel monkeys. He found

that within the midbrain most of the analyzed cells responded to self-produced vocalizations in a similar way as they did to the same vocalizations played back from an audiotape. Rather less than 10% of the cells showed no or only a weak response during the self-produced calls. By contrast, in the thalamus and in the auditory cortex a considerable number of neurons that reacted to playback calls did not respond to self-produced vocalizations. It seemed, thus, that higher stations of the auditory pathway display less activity during animal's vocal activity than lower ones. Two different functions were proposed for this selective neural processing. First, it could have a monitoring function required for controlling and learning species specific vocal performance. Secondly, calls are not of communicative value to the producer itself, and hence, the increasing number of cells in the higher auditory stations not engaged in the processing of self-produced calls would be free for analyzing essential signals coming from the environment. This would make these higher level cells appropriate for selective auditory attention to external sounds.

2.6. PROCESSING OF EXPECTED EXTERNALLY-INDUCED STIMULI

This section describes situations where an externally-induced stimulus has become, in a way or another, expected to the animal. These are probably the cases which most usually come to mind when examples of "expectation" are considered. As will be seen, there are several ways in which expectations can be created in experimental conditions but the focus here is, again, only in single cell studies.

Differential responses to expected vs unexpected stimuli. A simple way to create an expectation about an incoming event is by just telling beforehand to the human subject what it is that is going to happen in a minute or so. With animals one can set up similar expectations for a certain stimulus by employing the methods of associative conditioning. One can train the animals to form an association between the

delivery of a certain signal and an occurrence of another signal shortly after the first one (cf. second-order conditioning). If most of the time the following stimulus matches that which subjects were forewarned about, the subjective probability of the stimulus is high and the stimulus will be expected. If instead, a stimulus is presented contrary to the cues given beforehand, then the stimulus can be said to be unexpected to the animal.

Hocherman et al. (1981, 1990) trained rhesus monkeys to push a lever either to the left or right depending on whether they were presented an auditory signal of noise or tone, respectively. After the monkeys had mastered this task the behavioural paradigm was changed and additional light signals preceded the auditory ones. A flash of light on the left side signalled the occurrence of the noise signal (and a lever push to the left) and a light signal from the right preceded each tone stimulus. Now, it was possible for monkeys to predict the nature of the auditory stimulus based on the location of the visual signal. In a predetermined number of trials the auditory stimulus was preceded by the "wrong" visual signal. Responses of single units in the auditory cortex and the medial geniculate nucleus were recorded to tone and noise stimuli. Comparison between unit activity in true vs false conditioning trials revealed that on trials with correct behavioural responses half of the studied units were not affected by the predictability of the nature of the auditory stimulus. The other half was divided between neurons whose responses to the auditory stimuli were greater on true conditioning trials and neurons which responded more vigorously on false conditioning trials.

A set of blank trials were included in which the auditory stimulus was not preceded by a visual cue signal. Unit activity that was evoked on these trials was considered to represent the unit's base line response to the auditory stimulus. By comparing responses of a unit on cued trials and on blank trials, it was possible to describe the response features in terms of facilitation and inhibition. This analysis

revealed that in the subgroup of units whose responses were greater in true conditioning trials than in false conditioning trials, the responses were actually facilitated in the former case and inhibited in the latter case. A different pattern was found for units whose responses in false conditioning trials were greater than in true conditioning trials. These units showed a base-line response activity in true conditioning trials, but a strong facilitation in false conditioning trials.

These observations led the authors to suggest the existence of two neural mechanisms (Hoeherman et al., 1981). A signal-match detection mechanism involves units whose response to a correctly predicted stimulus is facilitated and whose response to a wrongly predicted stimulus is inhibited. An error-detection mechanism, on the contrary, includes units emitting a base-line activity to correctly predicted stimuli but showing strong facilitation to wrongly predicted (and hence unexpected) stimuli. These mechanisms are thus involved in the comparison of actual auditory signals with existing predictions about those signals. The authors proposed that such a comparison can be done if the realization of a particular prediction took the form of a specific spatial template of excitability through one or several levels of the auditory system. The observation that subcortical cells were affected by the effects of anticipation (Hoeherman & Yirmiya, 1990) suggested that 'anticipation-related' modulation of auditory information processing starts at the subcortical levels and that it is probably through descending corticothalamic projections that cortex controls the information processing in the lower levels of auditory system.

In a study by Beaton and Miller (1975) monkeys were taught to perform in an auditory reaction time task. This performance took place in two different experimental conditions. The monkeys were presented with high and low pitch tones, and in the first condition the monkeys were rewarded for rapid key releases to both tonal stimuli, irrespective of their pitch. In the second condition responses only to the high frequency tones were rewarded. In the behavioural paradigm these two condition

types were interleaved and the nature of the experimental condition was indicated to the monkey before the reaction signal with a light stimulus. In other words, responses to high tones were always rewarded, whereas responses to low tones were only rewarded in the condition where the pitch did not matter (signalled by the light cue). Single unit recordings from auditory cortex revealed that 25% of the sampled units showed definite alterations in responses to the same tonal stimuli under different experimental conditions. All these cells (except one) showed increased activity to the same low tone stimulus in the unrewarded condition relative to the responses evoked in the rewarded condition. No response modulation was observed to the high frequency stimuli which always signalled reinforcement. When trying to provide an explanation for their results Beaton and Miller (1975) stated that the "data do not fit easily within an attention or alerting model", because the monkeys had to attend to the stimuli in both conditions. They concluded that the activity of these neurons was correlated with a specific behavioural state which was a result of experimental conditions that controlled the monkeys' performance. Any other descriptions or definitions of this "behavioural state" were not offered.

By examining the results of Beaton and Miller (1975) against the effects of expectation one may offer a clearer explanation. It is plausible that after their animals had learnt that on most of the test trials releasing the key after a tone stimulus resulted a reward, the monkey was expecting (or hoping!) to receive an auditory stimulus signalling reward on every trial. Therefore, on trials when the requirement for the auditory discrimination was cued to the monkey, it was expecting to get a high pitch tone which would have meant a reward for key release. If, however, the delivered signal was a low frequency tone, this was unfortunate to the monkey (because it signalled no possibility to be rewarded) and against the monkey's expectations. Integrating the results to the model proposed by Hocherman et al. (1981) the modulatory effects observed by Beaton and Miller (1975) can be argued as reflecting the functions of "error-detecting mechanisms". The units belonging to this mechanism

had the property that they emit a baseline activity to correctly predicted stimuli but respond to unexpected stimuli.

Hypotheses about specific neural activity patterns created by expectation of particular sensory stimulation have gained experimental evidence in the studies by Freeman (1979). He found that the spatial pattern of EEG activity on the surface of the olfactory bulb in mice tended to be similar irrespective of the sensory input, whereas it changed to a new pattern when animals were expecting a particular odor. Freeman suggested that during learning, the pattern of neuronal activity which is induced by an odor provides the specification for a neural template in a form of strengthened connections between the neurons activated by that odor. After this learning phase the template could be activated by centrifugal connections in order to serve as a selective filter for expected odors.

The classical matching to sample paradigm can be seen as a task which requires that a neural template is formed from the sample stimulus and that the matching is based on comparing subsequent incoming sensory stimulation with this template. In this paradigm the subject is first shown a sample stimulus (a cue) and thereafter the subject is required to select a corresponding match stimulus from a number of possible stimuli. In other words the sample stimulus must be used to build up a kind of prediction about the subsequent matching stimuli, of which one is to fit to the prediction. Now, transferring this paradigm to neurophysiological experiments it is possible to study, for example, whether responses to matching stimuli depend on the preceding sample stimulus.

Haenny et al. (1988) recorded from neurons in the visual area V4 of rhesus monkeys which were trained to perform an orientation matching to sample task. The matching was either homo- or heteromodal. In heteromodal trials the animal was given a tactile sample (involving the subject feeling the orientation of a grooved plate

that it could not see). In homomodal trials the sample orientation was presented visually on the screen in front of the animal. The four matching stimuli were presented as a sequence of visual gratings and the animal was required to release a switch when it saw a grating whose orientation matched the sample orientation.

For over half of the neurons the visual responses to match stimuli were affected by the nature of preceding sample stimuli. The largest set of neurons was tested using the tactile-visual matching task. Two thirds of the neurons that were sensitive to both sample cue and match stimulus orientation showed a significant response interaction between cue and match stimulus orientation. About half of these neurons responded best to one of the four matching combinations in which both the cue and match stimulus orientations were the same (Fig. 2.11) and the other half responded best in a certain non-matching condition. No clear example was found of a neuron that responded well to each of the matching conditions but did not respond to non-matching conditions.

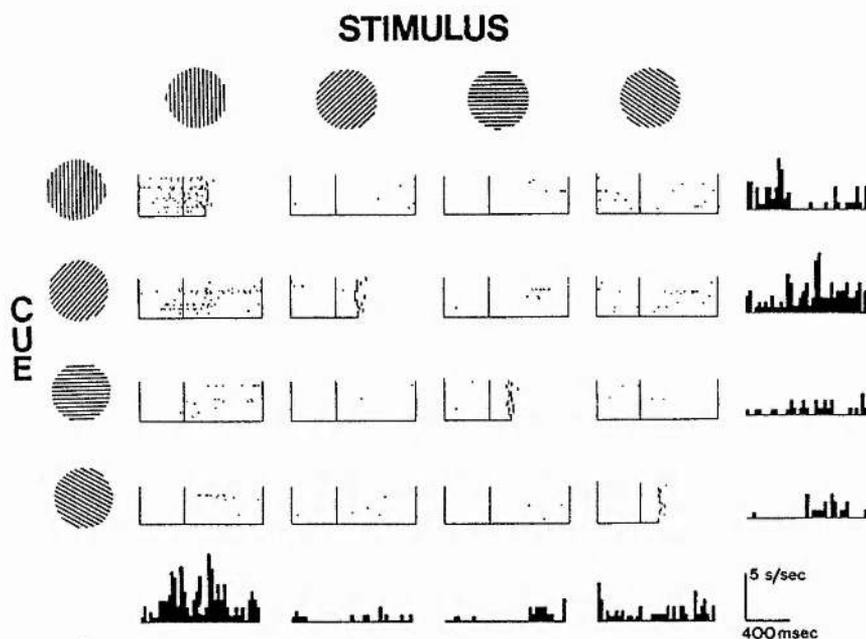


Figure 2.11. Response of a V4 unit that was selective for both stimulus and cue orientations. The rasterogram sets within any column are responses to the same stimulus orientation and the sets within any row are responses to different stimulus orientations after the animal was cued with a given tactile orientation. The histograms below and to the right of the array are summed responses. The coincidence of vertical cue and vertical stimulus was the only condition which produced a strong response with this particular cell. (From Haenny et al., 1988).

The results of visual-visual matching task were generally similar to those using the tactile-visual match. It is worth noticing that in visual-visual tasks the cue orientation was removed before the presentation of any stimuli. So, for example, cells were found whose responses showed sensitivity to a certain cue orientation, but to a different matching stimulus orientation, even though both were presented visually. Haenny et al. (1988) concluded that the cell tuning to cue orientation represented information specifically relevant to the matching task, rather than a basic sensory signal - either somatosensory or visual. Generally, the results provide support to the existence of "neural templates" created in the matching task in V4 and suggests that there are V4 units that are involved in comparing cue information to the actual stimulus information.

In the examples presented above, the expectations that the animals had, were formed because of a previous training in a certain type of behavioural task and, moreover, the expectations were likely to be present at a "conscious" level. However, it can be argued that natural every-day life is full of instances where a sensory experience is expected only at a "unconscious" level. Most environmental events are perceived and analysed by more than just one sensory channel, and this leads animals (and humans) to form intersensory associations. These associations can have a predictive function. For example, seeing an object approaching one's body signals an impending tactile sensation.

Mistlin (1988) and Mistlin and Perrett (1990) have recorded single-unit responses to tactile stimulation from the superior temporal polysensory area (STP) which is also high level somatosensory cortex in macaque monkeys. [The results regarding tactile stimulation resulting from animal's active exploratory movements have already been discussed in section 2.4]. They found that in about three quarters of the tested somatosensory neurons responses were stronger to tactile stimuli when the animal could not see (and hence expect) the approaching tactile stimulus. It is

relatively easy to see the functional importance for such mechanisms. As the authors suggest, when someone or something touches us from out of sight, there is a compelling sensation of being "touched" and this may indicate a need for interaction with another individual.

Anticipatory activity before stimulation. Still another effect of expectation on neuronal responses can be found in cases where changes (reflecting the expectation) in neuronal activity precede the actual stimulation of the sensory system in question. Single neurons in the dorsolateral prefrontal cortex (Sakai, 1974; Niki & Watanabe, 1979; Joseph & Barone, 1987), cingulate cortex (Niki & Watanabe, 1979), premotor cortex (Mauritz & Wise, 1986), primary motor cortex (Lamour et al., 1980) and caudate nucleus (Rolls et al., 1983; Hikosaka et al., 1989) have been shown to exhibit "anticipatory" activity changes preceding a task relevant stimuli. Extensive experience in performing a certain behavioural task is likely to lead to predictions about events within the task and it has been suggested that these neurons have a role in predicting environmental changes and preparing the animal for appropriate motor responses.

Recordings from the parietal cortex, superior temporal sulcus and frontal cortex of monkeys have revealed bimodal (visual and tactile) cells which give a visual response whenever the body part corresponding to the cell's tactile receptive field was approached by the investigator as though contact would be made (Hyvärinen & Poranen, 1974; Sakata, 1975; Leinonen et al., 1979; Mackay & Crammond, 1987; Mistlin & Perrett, 1990; Rizzolatti et al., 1981). As the visual and tactile receptive fields coincide it has been suggested that the function of these neurons is essentially predictive; i.e. providing information about the impending tactile collision and preparing the animal for an adequate behavioural reaction. In addition to passive stimulation the somatic anticipatory responses can be manifested during active movements of the animal as well. With the animal trained to reach and press an

illuminated button and then return its forearm to a rest plate, neurons sensitive to right arm approach have been found to respond as the monkey's arm is approaching the rest plate (Mackay & Crammond, 1987; cf. Mistlin & Perrett, 1990). Many neurons, mainly in area 7a, showed increased discharge rates immediately prior to the expected occurrence of a reward, a visual task cue, or on hearing the approaching footsteps of a familiar person (Mackay & Crammond, 1987). The authors considered the results to provide evidence for the presence of a nonsensory and nonmotor input providing "predictive information about immediately impending events of importance to the monkey". They regarded these approach responses as not reflecting a simple convergence of visual and somatosensory inputs, but postulated that the visual stimulus provided information to an 'internal model' which predicts subsequent events based on previous experienced associations.

CHAPTER 3

THE SUPERIOR TEMPORAL POLYSENSORY AREA IN THE PRIMATE VISUAL SYSTEM

3.1. INTRODUCTION

The principal object of this chapter is to describe the anatomy, connections and known physiological properties of the brain area that is the target of the neurophysiological experiments. The chapter starts with providing first a short overview of some of the anatomical and functional principles of visual processing within the primate cortex. This is particularly important because, as it will be seen later, the investigated brain area seems to be a site of convergence of separate information processing pathways within the cortex and consideration of the functional properties within these pathways is relevant to the present study. After the general overview, the scope is narrowed. The order of presentation of individual brain areas proceeds from describing the target area to include some other both anatomically and functionally closely related brain areas. This kind of order (rather than following hierarchy of processing stages from the bottom up) is deliberately selected in the belief that it guides the reader to a better understanding of the reasons for the particular experiments that are carried out in this thesis.

3.2. VISUAL PROCESSING WITHIN THE PRIMATE CORTEX

It is a general experience that when navigating ourselves about in the world we tend to be most dependent on the information that our vision mediates for us. In accordance with this, a large proportion of the cortical surface area is involved in the

processing of visual information. In primates it has been estimated that over a half (55%) of the total surface area of the neocortex is devoted to visual functions (Felleman & Van Essen, 1991). Visual information is not, however, processed uniformly over the cortical surface area devoted to vision. Anatomical, physiological and behavioural experiments in the monkey and man (Zeki, 1978; Macko et al., 1982, Newsome et al., 1985; Heywood & Cowey, 1987; Zeki et al., 1991) and clinical studies in humans with cerebral lesions (Damasio et al., 1980; Zihl et al., 1983; Goodale & Milner, 1992) have established by now that there exist several parallel processing pathways, each of which is relatively specialized for analysing and mediating one type of sensory information processing. It has been suggested that different neuronal systems extract information about form, colour, movement, and depth from visual sensory input (Livingstone & Hubel, 1987; Maunsell & Newsome, 1987; DeYoe & Van Essen, 1988; Zeki & Shipp, 1988).

Recently Felleman and Van Essen (1991) wrote an extensive review bringing together a large number of studies concerning visual areas and their connections in the macaque monkey. Based on neuronal response characteristics, presence of anatomical projections from known visual areas and distinctive architectonic tissue structure they reported a total number of 32 separate cortical areas implicated in the processing of visual information (Fig. 3.1). Of these 32 areas, 25 execute exclusively visual functions while the remaining 7 are visual association areas, being multimodal and receiving inputs from other sensory systems as well (Felleman & Van Essen, 1991). A total of 305 connections between these 32 visual areas have been found. A great majority of these pathways (242) involve reciprocal connections between areas and it is possible that this is the case with almost all of the remaining pathways as well, though evidence is so far missing.

Some of the pathways have been demonstrated to be only unidirectional. Felleman and Van Essen (1991) estimated that each visual area is connected on

average with 15 other areas. The density of the cortical connectivity varies, however. For example, V1 is linked to 9 other visual areas whereas V4 has connections with 21 areas.

Based on the laminar patterns of connectional origins and terminations between areas a hierarchy of visual areas has been proposed (Felleman & Van Essen, 1991). This hierarchy includes all the 32 visual areas organized at 10 different levels of cortical processing (Fig. 3.2). Areas at different processing levels are connected together with ascending and descending projections and areas at the same level are linked together with lateral connections. A typical feature in this hierarchy is that while some connections link areas at the immediately adjacent levels, the majority of the connections traverse more than 1 level, in an extreme case 7 hierarchical levels (V3-TF, see Fig. 3.2). The mean value for the number of traversed processing levels is 1.8. Another typical feature of the visual hierarchy is that most levels of the hierarchy have multiple different areas, especially in the middle portions of the hierarchy.

The presence of many areas at each level in this hierarchy is a manifestation of the existence of several parallel processing pathways mentioned earlier. Considerable attention has been given to the division of the visual pathways into two major processing systems: one directed ventrally from striate cortex into the temporal lobe and the other running dorsally into the parietal lobe. Ungerleider and Mishkin (1982) and Mishkin et al. (1983) were the first to suggest that the ventral processing stream is crucial for visual pattern and form analysis and recognition whereas the dorsal pathway enables the spatial location of objects. Another functional division based on this same anatomical organization has been made between form and motion analysis, the analysis of motion being taken care by the dorsal system (Livingstone & Hubel, 1987). In this context these two systems have often been referred to as P and M systems, respectively. This terminology reflects the anatomical segregation of these

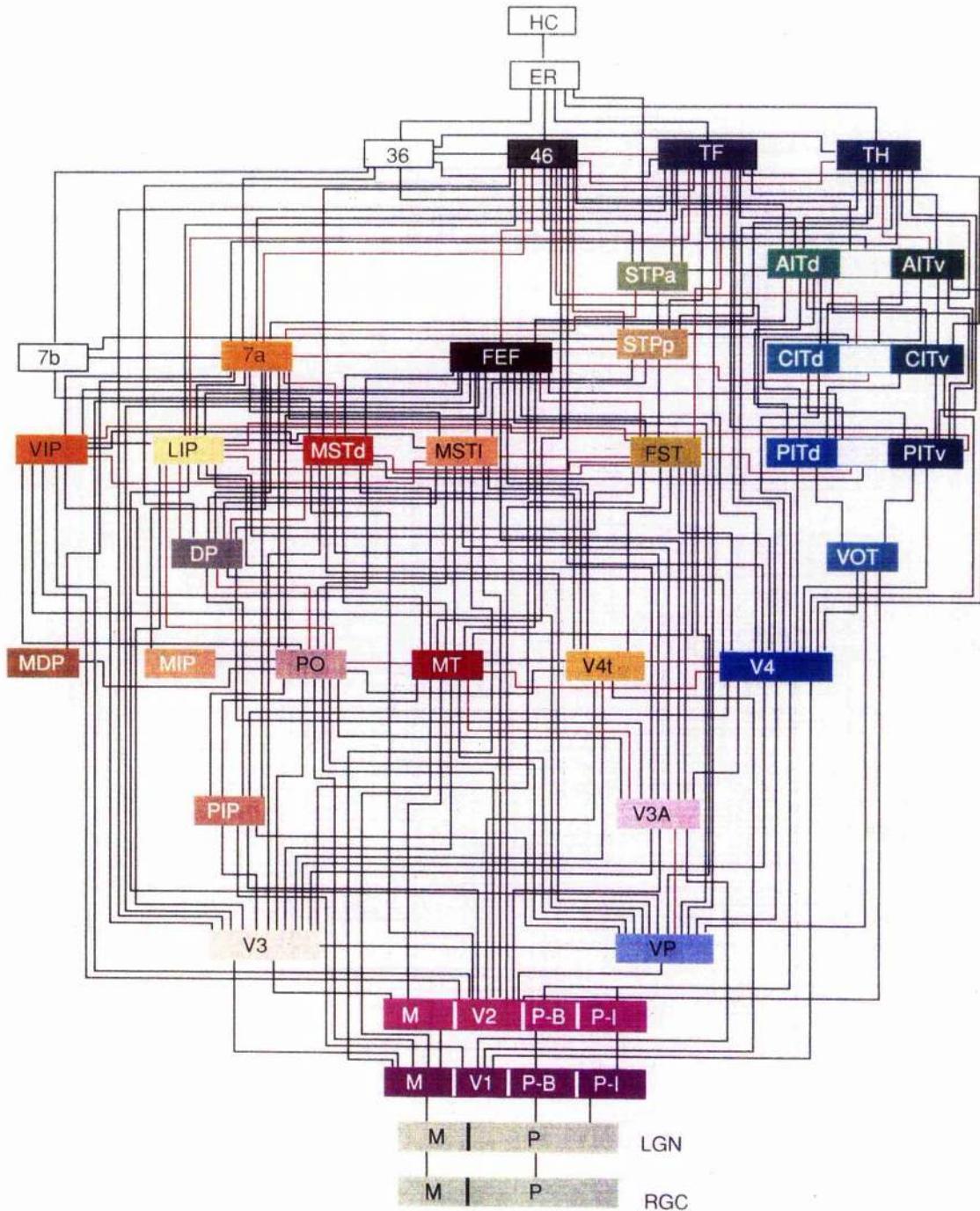


Figure 3.2. Hierarchy of visual areas. The hierarchy shows 32 visual cortical areas, coloured as in Fig. 3.1. Two subcortical stages (retinal ganglion cell layer and lateral geniculate nucleus) and several nonvisual areas are included into the hierarchy. (From Felleman & Van Essen, 1991).

subsystems at the level of lateral geniculate nucleus (LGN) where certain retinal ganglion cells sensitive to high spatial frequency (form information) project through parvocellular (P) layers and other cells sensitive to low spatial frequencies but high temporal frequencies (motion information) project through magnocellular (M) layers to the striate cortex.

The segregation between the two pathways is, however, far from being complete. At different stages of processing there is an extensive cross talk between the pathways which can take one of several types: i) cross talk within a single area by intrinsic circuitry, ii) convergence of ascending projections from two or more lower stage areas belonging to separate systems, iii) divergence of ascending projections to two or more higher areas in separate systems, iv) lateral projections connecting together two areas at the same hierarchical level but from separate systems and v) convergence/divergence in the descending projections tying areas in different subsystems together (Zeki & Shipp, 1988; DeYoe & Van Essen, 1988; Felleman & Van Essen, 1991).

In conclusion, the processing of visual input is largely distributed over the visual cortex which comprises of a network of numerous separate visual areas connected reciprocally together. Within this network of separate areas there exists a horizontal division of visual areas into hierarchically ordered processing stages as well as a vertical division of areas into separate processing streams. Within a processing stream progression from hierarchically lower stages to higher ones represents functionally a change towards more and more advanced processing being carried out. In terms of neuronal response properties this is reflected in an increased complexity of the response-triggering stimulus qualities as well as in an increased receptive field size. In different processing streams different attributes are analysed from the same visual input. For example, a sight of a red apple rolling on the top of a table may activate brain areas for very different reasons. Neurons in some areas may

become activated because there is something round in view, other neurons in other areas may respond because something red is in view and yet other neurons respond because something is moving, say, from left to right in the visual field.

3.3. THE ANATOMY AND FUNCTIONAL PROPERTIES OF SUPERIOR TEMPORAL POLYSENSORY AREA AND ADJACENT VISUAL AREAS

3.3.1. Architectonics

The classification of distinct areas within the primate cortex has evolved from two different lines of study. Histological studies have provided detailed brain maps based on regional cyto- and myeloarchitectonic criteria or connectional differences between areas, whereas other classification systems have emerged from observed differences in neuronal response properties between adjacent cortical areas. Therefore, there exist several overlapping classification systems with different terminology. The aim of this section is to provide a coherent picture of the areal organization within the anterior part of the STS as well as in some closely related brain areas by integrating different types of classification systems. Thereafter, in the following two sections when areal interconnectivity and neuronal response properties in different areas are described, the terminology will follow that used in the original papers. This way the reader can easily combine all the results from different studies into a unified entity while the existing heterogeneity and multiplicity is still retained. The classical organizations proposed by Brodmann (1905), Vogt and Vogt (1919) and von Bonin and Bailey (1947) are not presented except in cases where more recent studies have adopted the terminology from them.

Anterior dorsal STS. The superior temporal sulcus (STS) runs along the length of the temporal lobe splitting it dorso-ventrally into the superior temporal gyrus and inferior temporal gyrus (Fig. 3.3). Based on a cytoarchitectonic parcellation and intracortical

distribution of thalamic afferents Jones and Burton (1976) distinguished three rostro-caudally oriented fields on the surface of the superior temporal gyrus, one of which (T3) lay dorsally adjacent to the superior temporal sulcus and extended into the upper bank of the STS. Area T3 was observed to occupy the surface of the superior temporal gyrus in its anterior and posterior parts, and be buried elsewhere in the STS. Although giving but one designation to this whole area, Jones and Burton (1976) noted that T3 changed its architectonics within the STS.

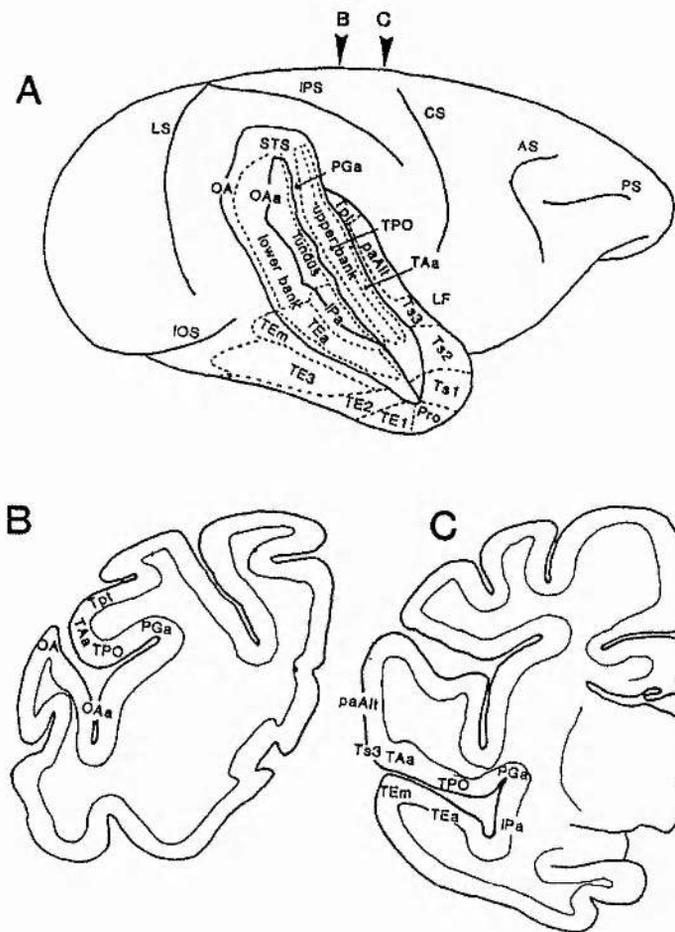


Figure 3.3. A) Lateral surface of the cerebral hemisphere of *Macaca mulatta* showing different architectonic areas in the temporal lobe. Superior temporal sulcus is opened for revealing both banks and the fundus of the sulcus. (PS = principal sulcus, AS = arcuate sulcus, CS = central sulcus, IPS = intraparietal sulcus, LS = lunate sulcus, IOS = inferior occipital sulcus). B) and C) Two coronal sections of the right hemisphere showing the architectonic parcellation within the superior temporal sulcus. Sections are taken at the levels as indicated by the arrows in Fig. A. (After Seltzer & Pandya, 1978).

Seltzer and Pandya (1978) investigated the cortico-cortical connections and the cyto- and myeloarchitectonic parcellation within the STS. These provided a clear differentiation between the areas of the superior temporal gyrus and those intrinsic to the STS. This work was an extension to the study by Pandya and Sanides (1973) in which they had already provided another classification of the superior temporal gyrus into five separate regions (Ts1, Ts2, Ts3, paAlt, and Tpt). Seltzer and Pandya further divided the upper bank of the STS into three different architectonic zones running along its rostro-caudal extent (see Fig. 3.3). Area TAa is differentiated from area Ts3 anteriorly and from area Tpt posteriorly. This area lies entirely within the upper bank of the STS. Area TPO is located medially to area TAa. Both areas TAa and TPO extend from about the level of the anterior tip of the central sulcus to beyond the most caudal point of the lateral fissure posteriorly. Area PGa is situated more medially to these areas. This third zone in the upper bank of the STS lies at the junction with the depth of the sulcus, also known as the floor or fundus of the STS. The rostral border of this area is difficult to define due to its location at the fundus but it may extend as far as TPO/TAa. More recently Seltzer and Pandya (1989b) have further subdivided area TPO into four subregions along its rostro-caudal extent (TPO1-4). Similarly, based on neuronal response properties and temporoparietal connections Harries and Perrett (1991) have shown area TPO comprised of large (3-4 mm) modules along its length.

Studying neuronal response properties Desimone and Gross (1979) and Bruce, Desimone and Gross (1981) showed that in contrast to cells in the inferior temporal cortex, cells in the upper bank and fundus of the STS are polymodal, and they referred to this area as the superior temporal polysensory area, STP. They defined area STP as lying in the upper bank of the middle and rostral regions of the STS and anteriorly crossing the floor of the STS. Based on architectonics and pulvinar afferents, STP was suggested to correspond area T3 of Jones and Burton (1976) and to overlap with areas TPO and PGa (Seltzer & Pandya, 1978).

In the areal organization of visual cortex by Felleman and Van Essen (1991) presented in Figures 3.1 and 3.2, this cortical area has been divided into two parts which they termed as anterior and posterior STP (STPa and STPp). This distinction was based on differences in cortico-cortical projections between the anterior and posterior parts of the STP as shown by Seltzer and Pandya (1989a,b) and Boussaoud et al. (1990). Together STPa and STPp occupy approximately 3.9 % of the total surface area of the visual cortex.

Caudal STS. In the caudal parts of the STS, anterior to the preoccipital gyrus, much of the cortex in the lower bank of the STS has been found to be architectonically similar to the cortex of the adjacent preoccipital gyrus named OA by von Bonin and Bailey (1947); Seltzer and Pandya (1978) also use this designation to refer to this part of the STS (see Fig. 3.3). Medial to area OA lies area OAa, which occupies the remainder of the posterior part of the lower bank and fundus of the STS. Anteriorly to area OAa, the rostral regions of the depth of the superior temporal sulcus are occupied by area IPa (Fig. 3.3).

The most commonly used classification system in the caudal parts of the STS has evolved from characteristic patterns of cortical connectivity between visual areas and their neuronal response properties (these will be described in the following sections). One of these areas (V5, Zeki & Shipp, 1988) is situated in the ventral (posterior) bank of the caudal STS, and as it is thought to be homologous to middle temporal visual area (MT) found in New World Monkeys, it has been termed MT in macaques as well (Allman & Kaas, 1971; Ungerleider & Mishkin, 1979; Van Essen et al., 1981). The lateral limit of area MT coincides with the area OAa (Seltzer & Pandya, 1978), but medially it continues beyond the limit of OAa to occupy also area PGa (Fig. 3.3). Desimone and Ungerleider (1986; Ungerleider & Desimone, 1986b) have further divided area MT into two sub-areas, MT and MTp, based on their differences in myelination and visuotopic representation.

The cortex medial to area MT (in the anterior or dorsal bank of the sulcus) has been termed medial superior temporal area (MST). This region differs from MT in its myeloarchitecture, cortical connectivity and functional properties (Van Essen et al., 1981; Maunsell & Van Essen, 1983; Desimone & Ungerleider, 1986; Ungerleider & Desimone, 1986b). Based on physiological response properties area MST has been further divided into dorsal and ventral sub-areas, MSTd (or "DSR" region in their original paper) and MSTv (Saito et al., 1986). Another division of MST has been provided by Desimone and Ungerleider (1986; Ungerleider & Desimone, 1986b) on the basis of its visuotopic organization, area MSTc representing the central visual field and area MSTp representing the peripheral field. Still a further terminology (MSTd and MSTl) has been used by Komatsu and Wurtz (1988) on the basis of differential cell responses related to tracking eye movements between these areas. Fortunately, it seems that all these sub-classifications of area MST coincide, i.e. MSTd coincides with MSTc and MSTv coincides with MSTp and MSTl.

Anterior to MT and MST in the fundus of STS lies an area with distinctive myeloarchitecture and visuotopic organization and it has characteristic neuronal response properties (Desimone & Ungerleider, 1986). Because of its location in the fundus of the STS this area was named FST (Fig. 3.4). Finally, based on the above mentioned criteria Desimone and Ungerleider (1986; Ungerleider & Desimone, 1986a) identified two further areas within the caudal STS, one located ventro-laterally to area MT (area V4t) and another dorso-laterally to area MST (area PP). Area PP has been divided further in two subregions. Based on functional properties of neurons Hikosaka et al. (1988) distinguished two regions in this area. An area labeled "mostly unresponsive region" lies in the middle third of the anterior bank more laterally to area MST, and the "caudal polysensory region" (cSTP) occupies the outer thirds of the anterior bank of the caudal STS.

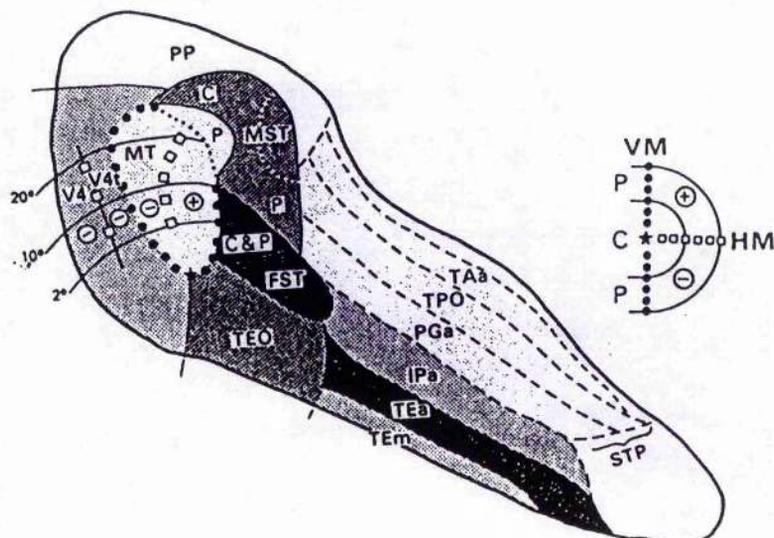


Figure 3.4. Location of the visual and polysensory areas in the superior temporal sulcus. The representation of the vertical meridian (VM) is indicated by black circles, the horizontal meridian (HM) by white squares, the fovea by a star, the upper visual field by a plus sign (+), the lower visual field by a minus sign (-), the central field by a C and the peripheral field by a P. (From Boussaoud et al., 1990).

In the classification system proposed by Felleman and Van Essen (1991) the terminology and areal organization follows the one just presented except that area MT has not been divided into two parts and area PP has been omitted from the classification.

Inferotemporal cortex. Ventral to the STS lies the inferior temporal gyrus. Seltzer and Pandya (1978) differentiated five rostro-caudally oriented zones (TEa, TEm, TE₁, TE₂ and TE₃) in this vast cortical area (see Fig. 3.3). Area TEa is situated entirely within the lower bank of the sulcus. The next area laterally is area TEm and it is located at the junction of the inferior temporal gyrus and it lines the lower bank of the STS. Areas TE₁, TE₂ and TE₃ occupy the ventro-lateral surface of the temporal lobe between the lower bank of the STS and the lateral wall of the occipitotemporal sulcus. These three areas correspond to one single area TE by von Bonin and Bailey (1947). Based on subcortical connections Iwai and Yukie (1987) have subdivided area TE along its rostro-caudal extent into three sub-areas, TEa, TEm and TEO (Fig. 3.5).

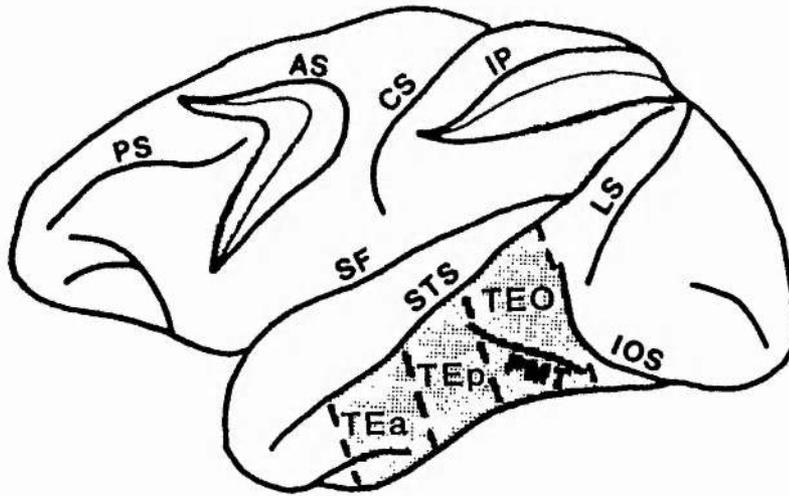


Figure 3.5. Lateral surface of the macaque brain with the location of inferotemporal areas. (From Morel & Buller, 1990).

In functional studies area TE has often been referred to as inferior temporal cortex (IT) (Gross et al., 1972; Desimone and Gross, 1979; Desimone et al., 1984) although differences in neuronal response properties along its extent have been reported (Desimone and Gross, 1979; Tanaka et al., 1991). In the map of cortical areas by Felleman and Van Essen (1991) inferotemporal cortex has been divided rostro-caudally into three parts, anterior, central and posterior IT, and each of these three areas has been further divided into dorsal and ventral sub-areas having thus three pairs of areas AITd/AITv, CITd/CITv, and PITd/PITv.

Posterior parietal cortex. Following the classical division of cortical areas by Brodmann (1905), area 7 in the inferior parietal lobule has been further subdivided into two areas based on cytoarchitectural criteria (Fig. 3.6). The caudalmost area has been designated to 7a by Vogt and Vogt (1919) or PG by von Bonin and Bailey (1947) and a more rostral area as 7b (Vogt & Vogt, 1919) or PF (von Bonin and Bailey, 1947). Pandya and Seltzer (1982b) have identified a transition zone between areas PF and PG, termed PFG, which they suggested to occupy the same position as Vogt and Vogt's area 7b. Like the inferior parietal lobule, the superior parietal lobule (area 5 by Brodmann, 1905) has been divided into rostral and caudal regions as well, areas 5a and 5b by Vogt and Vogt (1919) or areas PE and PEp by von Bonin and

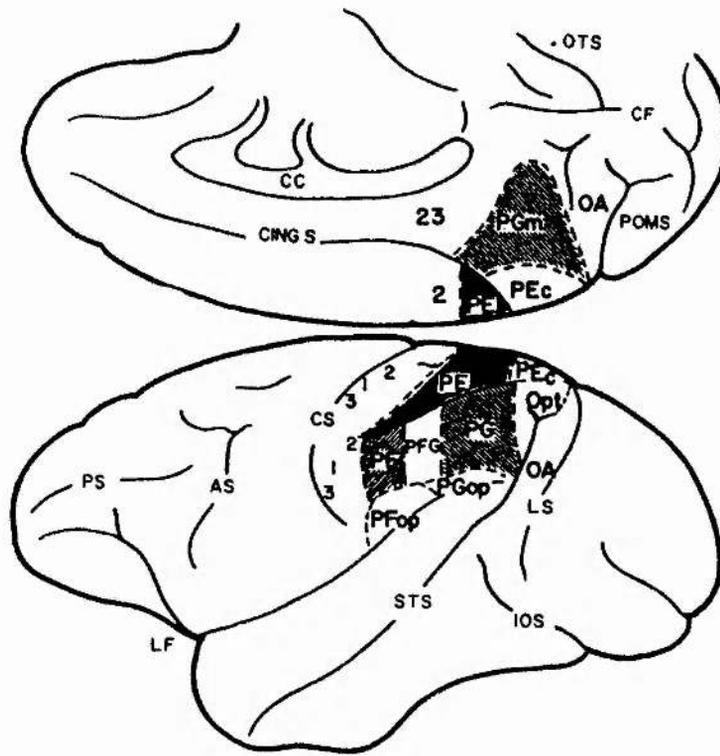


Figure 3.6. Lateral and medial views of the brain to show the architectonic parcellation of posterior parietal cortex. Abbreviations: PS = principal sulcus, AS = arcuate sulcus, CS = central sulcus, IPS = intraparietal sulcus, LS = lunate sulcus, IOS = inferior occipital sulcus, CING S = cingulate sulcus, CC = corpus callosum, CF = calcarine fissure, OTS = occipitotemporal sulcus, POMS = parietooccipital medial sulcus. (From Pandya & Seltzer, 1982).

Bailey (1947). In the areal classification system of Pandya and Seltzer (1982b) the caudal superior parietal lobule was designated as PEc. They also found an area in the medial surface of the parietal lobe which had an architectonically similar structure to area PG and which was hence termed PGM. In the hierarchy of visual areas constructed by Felleman and Van Essen (1991) presented in Fig. 3.2, areas in the superior parietal lobule are not included at all and in the inferior parietal lobule they identify only two separate regions, 7a and 7b.

3.3.2. Connections

This section concentrates mainly on describing the connections of the anterior parts of the superior temporal polysensory area between cortical and subcortical areas. In a few cases a brief description is given of the afferent projections to those cortical areas which send their efferents to the STP.

Area STPa is bilaterally connected to areas MST and FST in the caudal portions of the sulcus (Bruce et al., 1986; Boussaoud et al., 1990). Boussaoud et al. (1990) found anterogradely labelled terminals and retrogradely labelled cells from area TPO, PGa and IPa following injections of multiple tracers into area MSTc. In the same study area MSTp was found to send projections to the posterior portions of areas TPO and PGa and to receive projections from TPO, PGa and IPa. Contralaterally MSTc receives projections from TPO, PGa and IPa. Area FST was found to be bilaterally connected with PGa and IPa in the floor of the sulcus.

The rostral parts of the dorsal superior temporal sulcus receive projections from auditory cortex indirectly through the superior temporal gyrus (Jones & Powell, 1970; Seltzer & Pandya, 1978). The area paAlt in the superior temporal gyrus is connected to the areas TAa and TPO in the upper bank of the STS, and the caudally located gyral area Tpt projects to the areas TAa, TPO, and PGa.

The most caudal third of the inferotemporal cortex, area TEO, connects to the areas PGa and IPa, but not to TPO (Morel & Bullier, 1990). The more rostral parts of inferotemporal cortex, areas TEp and TEa, are connected to areas PGa and IPa, and the most rostral area TEa is connected to area TPO as well (Morel & Bullier, 1990; Baizer et al., 1991).

Several studies have demonstrated cortical projections from the parietal lobe to the temporal lobe (Pandya & Kuypers, 1969; Jones & Powell, 1970; Seltzer &

Pandya, 1978, 1984; Morel & Bullier, 1990; Harries & Perrett, 1991). The major source of parietal projections to the STS originates from a discrete region in the caudal third of the inferior parietal lobule, this area corresponding to the caudal portion of areas PG and Opt (Pandya & Seltzer, 1982b). This parietal area connects with areas TPO and PGa and IPa in the upper bank and fundus of the STS along their rostrocaudal extent. Modest projections also originate in mid-inferior (caudal PFG and rostral PG) areas and the medial surface of the parietal cortices PEc and PGm) terminating to the caudal segments of areas TPO and PGa.

Prefrontal cortex is reciprocally connected with the superior temporal sulcus. Connections exist between dorsolateral prefrontal cortex, area anterior to arcuate sulcus both dorsally and ventrally to principal sulcus, and rostral and middle regions of the STS (Jones & Powell, 1970; Pandya & Seltzer, 1982a; Pandya & Yeterian, 1985; Bruce et al., 1986). Pandya and Kuypers (1969) showed that prefrontal cortex dorsal to principal sulcus is especially heavily with the upper bank of the STS. Reciprocal connections exist also between STP and cingulate gyrus, and between STP and parahippocampal gyrus (Bruce et al., 1986).

The description of areal interconnectivity given above may suggest that some subareas (such as TPO and PGa) are sites for indiscriminate integration between numerous other cortical areas. As described in the preceding section, however, area TPO has also been subdivided into four subregions along its rostro-caudal extent (Selzer & Pandya, 1989b; Harries & Perrett, 1991). Studies of cortical connectivity between TPO and parietal cortex have shown that the projections from area TPO are organized into modules originating from distinct patches or bands of cells separated by patches without these particular connections (Harries & Perrett, 1991).

Apart from corticocortical connections superior temporal sulcus receives direct projections from thalamus. Burton and Jones (1976) showed that area T3

receives projections from the medial nucleus of the pulvinar which in turn receives projections from the deep laminae of the superior colliculus (Harting et al., 1980; Benevento & Standage, 1983). This may be the route through which visual information activates STP after striate lesions (Bruce et al., 1986; Gross, 1991). Subcortically both the upper and lower banks and the fundus of the STS send heavy projections to the amygdala, especially to the lateral nucleus (Aggleton et al., 1980), and to hippocampus (Insausti et al., 1987). The projection area from the STS extends from the most rostral parts caudally up to the level of posterior end of the lateral fissure. STP also sends direct projections to the ipsilateral pregeniculate nucleus (Ungerleider et al., 1984; Maioli et al., 1984).

3.3.3. Functional properties

This section concentrates mostly on describing the functional properties in the superior temporal polysensory area. Shorter descriptions are also provided for adjacent areas in order to clarify the role of STP in visual information processing and to explain what kind of information other areas are feeding to STP.

Area STP. Gross and co-workers (Desimone & Gross, 1979; Bruce et al., 1981) have provided detailed descriptions of the response properties of single neurons in STP by recording from anaesthetized monkeys. They found that ninety-six percent of the studied neurons were visually responsive and over half also responded to somesthetic or auditory stimuli. Of the neurons tested in all three modalities, 41% responded exclusively to visual stimuli, 21% responded to visual and auditory stimuli, 17% responded to visual and somesthetic stimuli, 17% were trimodal responding to all three modalities tested, and 2% were unresponsive. Multimodal response properties in this area have also been described by Baylis et al. (1987). Hikosaka et al. (1988) has examined the sensory properties of cells in the caudal parts of STP, area cSTP or STPp. This area also contains unimodal visual, auditory, and somesthetic cells, as

well as multimodal cells of two or all three modalities. Out of the 200 cells recorded by Hikosaka et al. (1988) 51% were unimodal, 18% were bimodal, and 2% of the cells were trimodal. Visual and auditory responses were more frequent than somesthetic responses so that the ratio of the population of cells driven by visual/auditory/somesthetic stimuli was 3:2:1.

Visual properties. Visual receptive fields in the STP cells are usually extremely large. Bruce et al. (1981, 1986) found that almost all receptive fields extended into both visual half-fields, and the majority approached the size of the entire visual field. They divided a sample of 256 units into three classes based on receptive-field size. Neurons in the class 1 (80%) responded to stimuli throughout almost the entire visual field. All neurons in this class had receptive fields that extended more than 30 degrees from the fovea in all directions. Half the neurons in this class responded similarly throughout most of their receptive field, but 34% were most responsive in the contralateral field, 4% in the ipsilateral, and 13% in the fovea. In size class 2, containing 14% (37) of the units, receptive fields were smaller, extending more than 30 degrees into only one or two quadrants of the visual field. Thirty-one of these units had receptive fields predominantly in the contralateral hemifield, and 21 of those fields were entirely contralateral. Nearly all of the predominantly contralateral fields were found near the posterior border of the recording area. Size class 3, 5% of the units, had the smallest receptive fields, extending less than 30 degrees from the fovea in any direction. In contrast to most units in the other classes, these units responded optimally to stimuli located at the fovea. In this study, the exclusively visual neurons proved to have smaller receptive fields (classes 2 and 3) twice as frequently as the polymodal neurons. The receptive fields of visual cells in area cSTP are also large but by contrast to the anterior portions of area STP two thirds are limited to the contralateral visual hemifield (Hikosaka et al., 1988). Receptive field diameter varies between 15 and 110 degrees (mean 59 degrees).

Most of the visual neurons in STP prefer moving to static stimuli (Fig. 3.7). Directional selectivity has been observed along the orthogonal axes (x, y, z). The cells have either a single preferred direction along one of the axes or they are bidirectionally sensitive with two preferred directions of motion 180 degrees apart (Bruce et al., 1981; Perrett et al., 1985b). The cells which respond to movement in depth (along z-axis) have also been found to respond to the expansion or contraction of a two dimensional spot of light (Bruce et al., 1981). Some cells prefer directions of movement radially symmetric about the center of gaze. About half of these respond to stimuli moving toward the center of gaze from any place in the peripheral visual-field, and another half respond to stimuli moving away (Bruce et al., 1981). One type

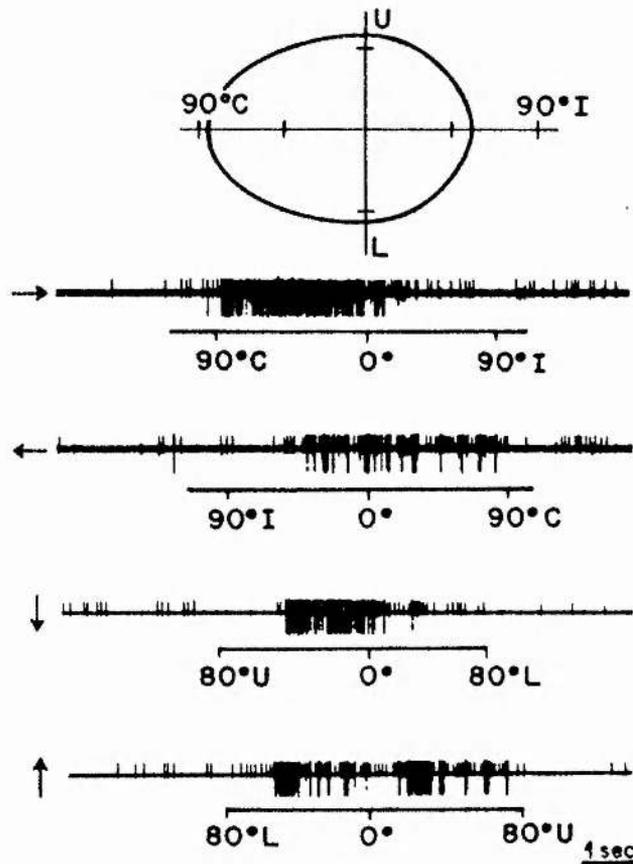


Figure 3.7. Visual receptive field of an STP neuron and responses to a stimulus (a white square) moved along each of the meridians in the direction indicated by the arrows. In the receptive field plot, the horizontal and vertical lines represent the meridians. The scale under each cell activity trace indicates the location of the stimulus. Abbreviations: C = contralateral, I = ipsilateral, L = lower, U = upper. (From Bruce et al., 1981).

of motion sensitive cells does not respond to translation but requires object rotation about one axis (x, y or z). These cells respond either to a single direction of rotation, or to two opposite directions of rotation (Perrett et al., 1985b). A further type of motion sensitive cells respond only to stimuli as they appear into or disappear out of the view (Bruce et al., 1981; Perrett et al., 1985b). Some of these cells are also directionally selective, i.e. they respond to an object entering the field of view from the subject's right. Comparably with the rostral STP, visual cells in the cSTP are often best activated by moving stimuli and most of the cells show directional selectivity as well (Hikosaka et al., 1988).

Smooth continuous stimulus movement over a wide velocity range (20-120 degrees/s) has been observed to be an adequate stimulus for most units. However, some units respond best to jerky movements giving a discrete response to each acceleration or deceleration of the stimulus (Bruce et al., 1981; Perrett et al., 1985b).

According to Bruce et al. (1981) most STP units, 70% of those they tested, have little or no preference for stimulus size, shape, orientation, or contrast. These non-selective units would respond similarly to spots and slits of light, to shadows, to slides and photographs of complex objects and to three dimensional objects. Form insensitive cell are also found in all types of movement sensitive cells (Perrett et al., 1985b; Mistlin & Perrett, 1990).

However, selectivity to very complex visual stimuli has been found in the STS units. The most interesting ones are units selective for faces, bodies, and body movements (Bruce et al., 1981; Perrett et al., 1982, 1984, 1985a,b, 1987, 1989a,c, 1990a,b,c, 1991, 1992; Rolls & Baylis, 1986; Hasselmo et al., 1989; Harries & Perrett, 1991; Gross, 1992; Hietanen et al., 1992). The "face-selective" cells respond usually to both human and monkey faces, whether real or projected, and they have relatively long response latencies, ranging from 70 to over 200 milliseconds (mean

120 ms, Oram & Perrett, 1992). The responses are usually relatively constant despite several stimulus transformations, such as isomorphic rotation, colour, size, distance, contrast or lighting conditions (Perrett et al., 1984; Hietanen et al., 1992). However, head orientation (Perrett et al., 1989a,c, 1990c, 1991; Hasselmo et al., 1989), gaze direction (Perrett et al., 1990c, 1992), and identity and expression (Perrett et al., 1984; Hasselmo et al., 1989) have been observed to affect responses (Fig. 3.8).

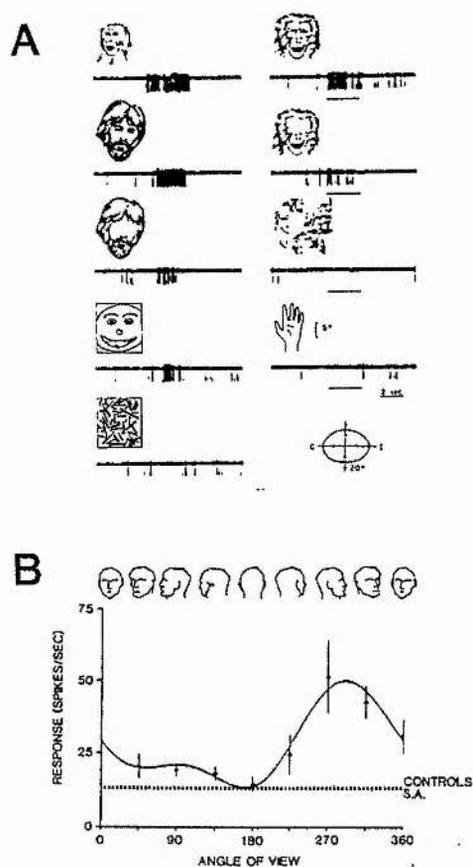


Figure 3.8. Responses of STP neurons showing selective responses for faces. **A)** An STP unit that responded better to human and monkey faces than to all other stimuli tested. Stimuli on the left were photographs or drawings which were swept across the fovea. Stimuli on the right were presented as static slide pictures. Removal of the eyes or presenting the face as a caricature reduced the response. Rearrangement of the facial features abolished the response completely. (From Bruce et al., 1981). **B)** Responses of an STP neuron showing response selectivity for the right profile of a head. The mean responses (+/- 1SE) are illustrated to 8 views of the head. The curve represents a best fit cardioid function, relating response to view. Dashed lines are the mean responses to control stimuli and spontaneous activity. (From Perrett et al., 1991).

Recordings from the area between the caudal parts of STP and MST have revealed three quarters of cells to be unresponsive to any stimulus and hence the area has been labeled as the "mostly unresponsive region" (Hikosaka et al., 1988). A quarter of the cells in this area respond to only visual stimuli. These visually responsive cells have been further classified into unidirectionally selective cells (39%), pandirectional (35%) movement sensitive cells, and to cells which also respond to stationary stimuli (Hikosaka et al., 1988). Visual receptive fields were large so that a half had receptive fields extending into both visual hemifields. Some directionally selective cells were found to respond only to movements of real faces, hands, bodies, or other complex three dimensional objects (Saito et al., 1986; Hikosaka et al., 1988).

Auditory properties. Benevento et al. (1977) reported that 13% of the units they tested in area STP were responsive to auditory stimuli alone, and another 36% of tested cells were bimodal giving both visual and auditory responses. Auditory stimuli elicited both ON and OFF -type responses. An excitatory OFF-response was often preceded by an inhibition to the onset of a tone. For many of the cells the inhibitory effect was selective to the frequency of the tone. In bimodal units auditory responses were observed to interact with visual ones and, for example, auditory stimulation could suppress excitatory responses to coinciding visual stimuli very effectively. Bruce et al. (1981) did not find any unimodal auditory units from area STP. Clicks, tones, and vocalizations were all effective stimuli for most multimodal units responsive to auditory stimuli. A minority of cells responded best to certain sounds. Some units showed preference for contralateral auditory stimuli over ipsilateral ones. Again, in a few cases complex bimodal interactions between auditory and visual stimulation were observed. They found, for example, a unit which responded only to coinciding sight and sound of an object striking a surface. In the caudal parts of area STP auditory cells have large but definable receptive fields which mostly located in the contralateral auditory hemifield (Hikosaka et al., 1988). Most cells respond

similarly to several auditory stimuli, such as pure tones, white noise, human voices and hand clapping. Few cells showed selectivity for complex sounds.

Somatosensory properties. Mistlin (1988) and Mistlin and Perrett (1990) reported about one fifth of the recorded units in STP to be sensitive exclusively to somesthetic stimulation. According to response properties three classes of somatosensory responses were distinguished. Tactile cells were responsive only to cutaneous stimuli, joint cells responded to passive joint movements and vibration cells to vibration on the skin. There were also convergent neurons which comprised those cells with sensitivity to more than one submodality. Tactile cells were observed to lack any selectivity to simple stimulus parameters such as object shape, size, or texture. Receptive fields were large covering often the whole body; for example, joint movement sensitive cells were responsive to the passive rotation of any joint. Similarly, in the study by Bruce et al. (1981) cells which responded to cutaneous stimulation were observed to have almost always large and bilateral receptive fields, covering often the entire body surface. Usually any type of stimulus, pressure, stroking, or blowing would elicit a response. Many of the somesthetic units were extremely sensitive, responding even to bending of a single hair.

In addition to these "conventional" somesthetic properties Mistlin (1988) and Mistlin and Perrett (1990) reported that tactile responses could be modulated by the degree to which the monkey could expect the occurrence and nature of tactile stimulation. Active exploratory hand movements made by the animal itself were found to produce no tactile responses when the monkey contacted familiar, expected surfaces such as its own body or highly familiar items within reach, whereas equivalent tactile stimulation as a result of encountering novel, unexpected surfaces produced vigorous neuronal responses. When touched passively by the experimenter the stimulation could be expected or unexpected depending on whether the monkey could see the approaching tactile stimulus. A great majority of the tested cells

produced significantly stronger responses to unexpected tactile stimulation out of sight as compared to similar stimulation in sight. The response properties of these cells have already been considered in chapter 2 in sections 2.4 and 2.6.

In the caudal parts of area STP somesthetic responses can also be elicited by various tactile stimuli. Hikosaka et al. (1988) classified four different receptive field types based on their extent and location. These varied from small fields limited to a part of the contralateral arm to wide size fields covering both sides of the body. A half of the receptive fields of different modalities in multimodal cSTP cells were found to be overlapping. The other half was divided between complementary (no overlapping) and partially overlapping receptive fields. In a small number of multimodal cells a cross-modal correspondence for the movement selectivity (e.g. direction) of the stimuli between different modalities was observed (Fig. 3.9). Similar cross-modal correspondence has also been found in the rostral parts of area STP. Mistlin and Perrett (1990) observed that some neurons responded visually to approaching stimulus movement and to touch onset whereas other units responded to retracting stimulus movement and to touch offset.

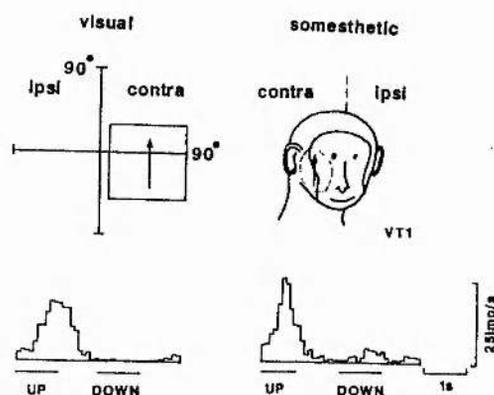


Figure 3.9. A cross-modal matching for upward movement of visual and somesthetic stimuli in a bimodal cSTP cell. Upper panels show the visual and somesthetic receptive fields. Lower panels illustrate peristimulus time histograms of the cell responses for a randomly textured pattern moving upwards and for a somesthetic stimulation by stroking the hairs with a thin object (right). (From Hikosaka et al., 1988).

Lesion studies by Luh et al. (1986) have suggested a role in attention control and visually guided reaching and grasping movements for STP. Unilateral lesions produced impairments in orienting to visual, auditory, or tactile stimuli, as well as clumsiness and inaccuracy in food reaching. These deficits were transient, however, and disappeared within 5 weeks. A second lesion to the intact hemisphere produced more severe and longer lasting neglect symptoms and deficits in exploratory movements. Similar results have been reported by Petrides and Iversen (1979). Aggleton and Mishkin (1990) have shown that a combined STP and area TE lesion leads to some signs of a classical Klüver-Bucy syndrome (a tendency to touch and manipulate inedible objects and an absence of emotional reactions to aversive visual stimuli) which follows amygdectomy. These results were suggested to indicate that both areas STP and TE "provide the amygdala with the information needed for visual identification of the inedibility and aversiveness of objects".

Ventral bank of the STS and IT cortex. Desimone and Gross (1979) showed the lower bank of the STS to contain cells responsive only to visual stimulation, which lies in striking contrast to the dorsal bank of the STS. The visual receptive fields were found to be on average smaller in size compared to receptive fields of STP cells, varying, however, from very small (1 x 1 degrees) to very large (80 x 130 degrees): the median RF size was approximately 25 x 25 degrees. Receptive fields usually included the fovea, and even though the receptive field centers were located in most cases within the contralateral visual field, the large majority of receptive fields extended into the ipsilateral hemifield. The inferotemporal cortex is not visuotopically organized. The size of the receptive fields tends to be larger in the anterior portions of the IT than in the remainder of the IT (Gross et al., 1972; Desimone & Gross, 1979; Tanaka et al., 1991).

The responses of IT neurons have been observed to be selective to the size, shape, texture, orientation or colour of the visual stimuli (Gross et al., 1972; Gross et

al., 1979; Sato et al., 1980; Desimone et al., 1984; Tanaka et al., 1991; Komatsu et al. 1992). A few IT units have been found selective for specific objects such as hands and faces (Gross et al., 1972; Perrett et al., 1982; Desimone et al., 1984). The ventral bank of STS (area TEa) has been reported to contain units selective to the sight of different specific manipulative actions of hands (Perrett et al., 1989b,c,d). Like units sensitive to the sight of faces these cells generalize across different viewing conditions including distance, speed and orientation. The critical response triggering feature is that the manipulative actions involve the interaction between a hand (or hands) and an object. Comparable hand actions without an object or hand movements without making physical contact with an object in view, cease to activate these units.

A recent study by Tanaka et al. (1991) has shown, however, that the cells with different response characteristics are not distributed uniformly over the inferotemporal cortex area along its rostro-caudal extent. They found that cells in the posterior part of IT (area TEO) could be activated maximally by simple stimuli, bars and disks, just by adjusting the size, orientation or colour of the stimulus. Instead, cells in the anterior 2/3 of IT (areas TEa and TEp) required more complex features for their activation. These features were such that they could be present as partial features in images of several different natural objects (see Fig. 3.10).

The response of some IT units has been shown to be modulated by the animal's selective attention and a role in memory processes has been suggested for IT neurons as well (Fuster & Jervey, 1981; Moran & Desimone, 1985; Baylis & Rolls, 1987; Miyashita & Chang, 1988; Sakai & Miyashita, 1991). Baylis and Rolls (1987) found that about a quarter of the visually responsive neurons showed a different response to the first and second presentations of the same stimulus. This differential response was sustained over a delay period provided that no other stimuli were presented between the "novel" and "familiar" presentations of a test stimulus, but in

most cases even one intervening stimulus prevented the differential response from occurring.

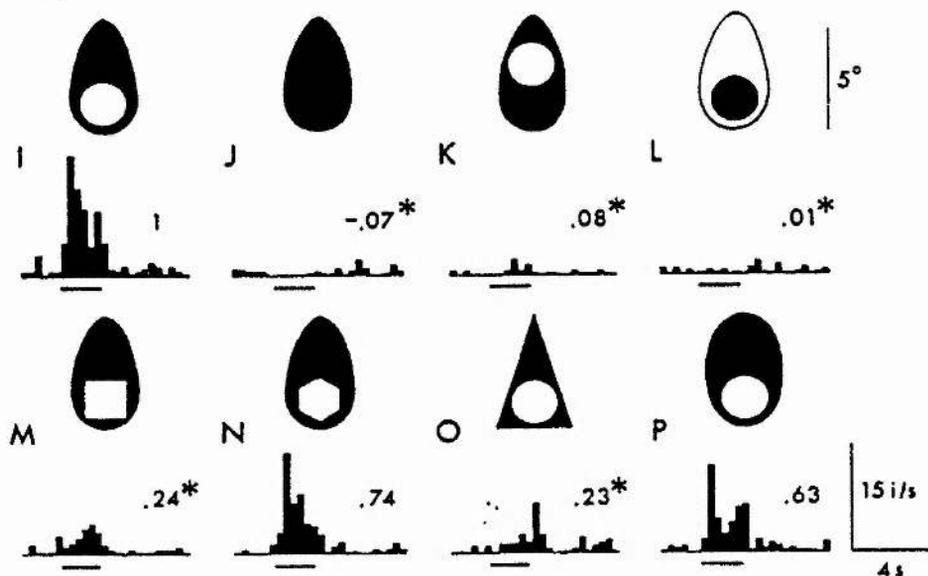


Figure 3.10. An IT cell responding to a combination of a dark ovoid and a light disk within the ovoid. (From Tanaka et al., 1991).

Sakai and Miyashita (1991) have suggested that inferotemporal cortex may contain neural mechanisms for storage and retrieval in long-term memory. They trained a monkey to associate a certain stimulus picture with another one through repeated trials in a pair-association task. Single-unit recordings revealed that training in the paired-associate task had modified the responses of neurons in the anterior and ventral parts of the temporal cortex so that single cells gave selective visual responses to both stimulus pictures of a certain (original) pair when they were used as a cue, even if the pictures had no apparent geometrical similarity ("pair-coding neurons"). The responsivity of some other cells seemed to be connected to the activity of retrieval processes as they exhibited enhanced activity during the delay period after the presentation of a cue stimulus. Again, both stimulus pictures in the originally learned pair-associations were able to elicit the enhanced delay activity ("pair-recall neurons").

Visual areas in the caudal STS. Area MST has been shown to contain a high proportion of direction selective cells. It has a crude retinotopic organization and its receptive fields are relatively large in size: largest receptive fields are on average 100 x 100 degrees in size, and in some cases fields extend deep into the ipsilateral side as well (Zeki, 1980; Van Essen et al., 1981; Desimone & Ungerleider, 1986; Saito et al., 1986; Duffy & Wurtz, 1991a,b).

Three categories of directional selective cells has been classified in area MSTd (Tanaka et al., 1986; Saito et al., 1986; Hikosaka et al., 1988; Duffy & Wurtz, 1991a). One class consists of cells responsive to a straight movement in the frontoparallel plane with unidirectional selectivity. The second class includes cells responding to an expanding or contracting size change of patterns. The third class of cells has two subgroups: cells responsive to a unidirectional rotation of patterns either in the frontoparallel plane or in depth. A large fraction of the cells within each category prefers the movement of a wide field to movement of a small object (see Fig. 2.5). Duffy and Wurtz (1991a) found that a vast majority (62%) of the neurons within MSTd responded to a combination of either two or all three stimulus motion types.

In area MSTv the vast majority of the directionally selective cells prefers a straight movement in the frontoparallel plane and in contrast to cells in the MSTd, they prefer the movement of a small object to the movement of a wide texture field (Tanaka et al., 1986; Sugita et al., 1990). It has been found that the cells in MSTv can be activated by placing a stationary object in front of the large moving field texture and that this activation is due to both the disappearance and appearance of components of the background at the object border and the movement of a large field background (Sugita & Tanaka, 1991).

It has been suggested that the cells in MSTd are involved in the analysis of visual field flow such as would be caused by self-movement of the animal whereas

cells in the MSTv extract the movement of an object in physical space (Saito et al., 1986; Tanaka et al., 1986; Roy & Wurtz, 1990; Saito, 1992). Area MSTd has been shown to contain cells responding to visual stimuli especially during smooth pursuit eye movements and they exhibit an extraretinal input in addition to the visual signal. A role in maintenance of ongoing pursuit movement or in perception of spatial relationships between the subject and the environment has been suggested for these MST cells (Komatsu & Wurtz, 1988a,b; Newsome et al., 1988). These functional properties have been dealt with in more detail in the context of self-motion in chapter 2 (section 2.2).

Desimone and Ungerleider (1986) recorded from area FST cells and found that 32% of the units were directionally selective. In addition to this they found cells which could be driven only by complex motion of three dimensional objects. Area FST lacks visuotopic organization and the receptive fields are large (up to 50 x 50 degrees) often crossing into the ipsilateral visual field.

Area MT is probably the most extensively studied extrastriate visual area, and electrophysiological recordings have repeatedly shown it to be specialized for the analysis of visual motion in macaques (Dubner & Zeki, 1971; Zeki, 1974; Van Essen et al., 1981; Maunsell & Van Essen, 1983a; Albright, 1984; Tanaka et al., 1986; Desimone & Ungerleider, 1986). Psychophysiological studies have shown thresholds for perceiving movement in random dot patterns to be elevated in macaques after lesions of area MT (Newsome & Pare, 1988). Even more interestingly microstimulation of directionally selective cell columns has been shown to bias the animal's report of the direction of motion in a random dot display towards the direction of motion encoded by the stimulated neurons (Salzman et al., 1990).

The general feature of area MT neurons is that they respond better to moving stimuli than to stationary stimuli, and the majority of them are exclusively selective to

one direction of motion (Fig. 3.11). Maunsell and Van Essen (1983a) reported that on average the response rate falls to half-maximum when the direction of movement deviates 30 degrees from the best direction. Directional selectivity is independent of stimulus color, shape, or length. High proportion of the cells also shows selectivity to stimulus orientation although the responses are usually weaker to stationary-oriented stimuli than those to moving stimuli, and a bar of any orientation evokes a near maximal response as long as it is moving in the preferred direction. A common observation is that orientation preference tested with stationary bars is either perpendicular or parallel to the preferred direction of movement (Van Essen et al., 1981; Maunsell & Van Essen, 1983a; Albright, 1984).

Most units are also tuned for the speed of the stimulus motion. Maunsell and Van Essen (1983a) observed preferred stimulus speeds extending from 2 to 256 deg/sec while the average was 32 deg/sec. The receptive field size is very variable.

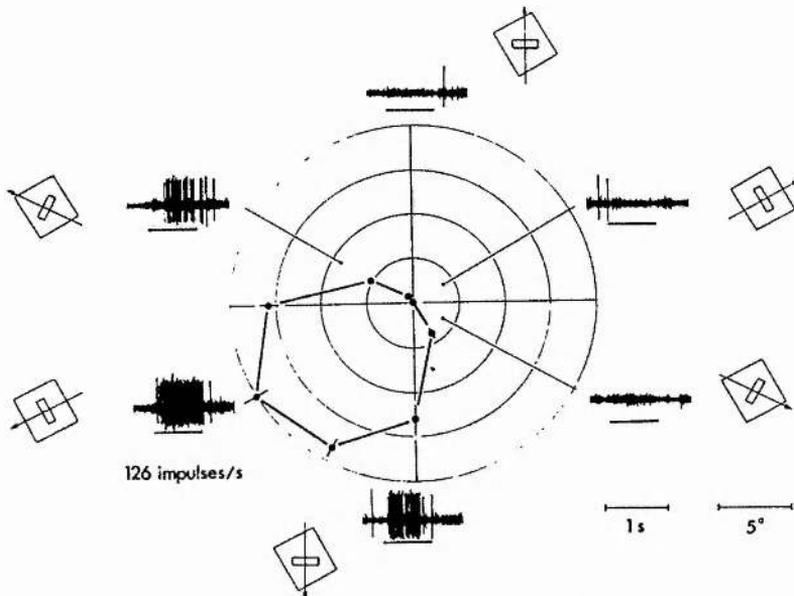


Figure 3.11. Direction selectivity of a single neuron in area MT. Oscilloscope records show individual responses to the six indicated directions of motion. The size of the stimulus and its direction relative to the receptive field outline are indicated alongside each trace. The polar plot is the average rate of firing during stimulus presentation for five repetitions for 12 directions of motion. The standard error of the mean is given for each direction. (From Maunsell & Van Essen, 1983a).

Area MT contains a complete, topographic representation of the contralateral visual hemifield (Zeki, 1974; Ungerleider & Mishkin, 1979; Van Essen et al., 1981), and the representation of direction of motion appears to be systematically arranged in vertical neuronal columns (Zeki, 1974; Maunsell & Van Essen, 1983a; Albright et al., 1984). Generally receptive fields are smaller than in area MST but much larger in size compared to receptive fields in area 17 (Zeki, 1974; Desimone & Ungerleider, 1986). The receptive field sizes range from very small (about 2 x 2 degrees) to very large (40 x 40 degrees) receptive fields (e.g. Fig. 4 in Desimone & Ungerleider, 1986).

Tanaka et al. (1986) have shown the responses of MT cells to be affected in various degrees by the stimulation in the classical receptive field surroundings. The distribution of the strength of this effect was observed to be continuous across a cell population, but Tanaka et al. (1986) arbitrarily differentiated two kinds of receptive field properties in MT cells. One group of cells has excitatory center receptive fields which are surrounded by the inhibitory fields. Movement in the inhibitory field occurring in the same direction as in the central field is able to suppress the responses to the central movement, whereas movement in the opposite direction has no effect, or in some cases even facilitates responses to the central stimulus movement (see Fig. 2.3). The other group of cells responds to wide-field movement as well as to stimuli confined within the excitatory field. The receptive field properties of MSTd cells have been suggested to be constructable by converging signals from MT cells (Saito et al., 1986).

In addition to the role of area MT in the perception of visual movement a role in the guidance of eye movements has been proposed. Lesions restricted to area MT have been shown to impair eye movements to moving visual stimuli while leaving eye movements to stationary targets intact (Newsome et al., 1985). In electrophysiological studies area MT has revealed neurons which discharge more strongly during smooth

pursuit of small moving targets than by visual stimulation during fixation (Komatsu & Wurtz, 1988a, b; Newsome et al., 1988). These cells are directionally selective, and the preferred direction for visual motion coincides with the direction of the pursuit eye movement. The pursuit-related response of these cells depends on visual stimulation of the retina by the "slipping" pursuit target. Taken together, lesion and electrophysiological studies suggest that area MT participates in controlling of eye movements to moving visual stimuli by providing visual motion information to the pursuit system.

Posterior parietal cortex. Many parietal cells seem to integrate eye position and retinotopic visual information providing thus a basis for neural mechanisms for spatial constancy (Andersen et al., 1985, 1987). Single cell recordings performed in area 7a have shown that visual space is not mapped solely in retinal coordinates nor in head-centered coordinates. The visual receptive fields move with the eyes but the responsiveness of these units to retinotopically identical stimuli varies as a function of the eye position in the orbit.

A role in sensory-motor integration has been considered to be one of the major functions of the inferior parietal lobule. Recordings from this area have revealed neurons which are maximally active during motor and oculomotor behaviours of animals (Hyvärinen & Poranen 1974; Mountcastle et al., 1975; Lynch et al., 1977; MacKay & Crammond, 1987; Taira et al., 1990). For the present work it is of particular importance that the activity of some parietal neurons has been found maximally correlated with reaching movements under visual guidance. Therefore, a role in monitoring (rather than in commanding, cf. Mountcastle et al., 1975) the ongoing motor activity has been assigned to these parietal neurons (Taira et al., 1990).

As in the inferior temporal cortex, many of the parietal visual neurons show also enhanced responses to overtly or covertly attended stimuli independent of any

subsequent eye or hand movements (Lynch et al., 1977; Robinson et al., 1978; Bushnell et al., 1981).

CHAPTER 4

SUMMARY OF THE LITERATURE REVIEW AND RATIONALE FOR THE PRESENT EXPERIMENTS

Towe (1973) wrote:

The old view of the mammal as a passive receiver and responder has long since been supplanted by our current view of the mammal as an active experienter. In interacting with its environment, the mammal seeks input and indeed "expects" specific inputs, especially as a consequence of specific output.

The inquiry into the neurophysiological (neuronal) signs of expectation was begun by investigating how the nervous system handles self-produced stimulation. It was shown that the nervous system separates self-produced stimulation from externally-induced (unexpected) sensory input in many different modalities and at many different levels. Expected re-afferent signals caused by an animal's own actions can contain useful information for controlling the animal's ongoing motor activity. For example, visual signals received during locomotion are used in controlling posture and providing information about one's own movements in relation to the environment (Lee & Aronson, 1974). In other instances, however, self-induced stimulation provides no useful information and it may actually interfere with the processing of environmental signals. This was the case with the visual motion input resulting from an animal's own eye movements or auditory processing of self-vocalization. In these cases parts of the nervous system seemed to ignore or gate out the self-induced reafferent signals.

Visual whole-field movement signals which result from an animal's own locomotion are processed in a separate motion processing systems from the

processing of motion of local external objects. Whole-field movement is preferentially processed compared to localized motion within the brainstem level (in the AOS and vestibular nuclei) and similar discrimination is present among the highest cortical stages of visual motion processing, in areas MT and MSTd. Moreover, it has been shown that the motion processing system devoted to whole-field movement (i.e. resulting from ego-motion) does not work in isolation from the other locomotion signalling sensory systems. Vestibular and somatosensory systems interact with the visual processing at the level of vestibular nuclei, thalamus and cortex. Some indication of the vestibular-visual interaction occurring in area MST was found by Thier and Erickson (1992).

Despite the early (and even relatively recent) attempts to explain the visual stabilization during eye movements by referring only to corollary discharge type of mechanisms, it is now known that retinal mechanisms (i.e. whole-field movement) play as an important role as the motor mechanisms in this process. In the case of saccadic eye movements (which must be considered separately from smooth pursuit movements) both mechanisms are present in a very early processing stage, in the superior colliculus. Visual motion processing during smooth pursuit is a more complicated problem, because *smooth pursuit movements do not occur naturally unless there is a moving object in view*. As was discussed, pursuing a moving object against a static background actually elicits a sensation of the movement of the background (Filehne illusion) which shows that the stabilization mechanisms during smooth pursuit do not work perfectly. The finding was that at the cortical stages where neurons generally respond to retinal motion velocities that occur during smooth pursuit sweep there are cells which respond selectively to object motion across a stationary retina (real motion) and that the number of these cells increases as one moves higher and higher in the hierarchy of cortical visual stages. Again, both retinal and extraretinal mechanisms are involved in the stabilization. Even though there was some controversy between studies concerning the first stages where "real-motion" is

separated from self-induced retinal motion (Erickson & Thier, 1991 vs Galletti et al., 1984, 1988, 1990), it appears that the major extraretinal input may not be integrated with visual motion cells before area MST. This is supported also by the findings that area MST receives extraretinal input in order to participate in smooth pursuit control. In area MT the pursuit cells receive only retinal "slipping" signals (Komatsu & Wurtz, 1988a,b; Newsome et al., 1988).

It is obvious, however, that the illusory perception of background movement during smooth pursuit can not be solely contributed to by the whole-field sweep across the retina as there is another very powerful motion cue present, i.e. relative movement between the moving object and the background. The latter motion cue is also present during locomotion in a three-dimensional static environment. Ego-motion provides thus not only whole-field signals, but local motion cues as well depending on the image distances of objects in the environment. It was shown that the thresholds to detect object-motion are elevated when the visual (or vestibular or somatosensory) system is fed with typical self-motion cues (Probst et al., 1986). This may reflect the difficulty of the task that the visual system faces in a situation when the animal is locomoting and there *really is* local movement present as well (relative to the stationary environment).

The studies describing somatosensory processing showed first that active movements *affect* to the processing of somatosensory information and, again, that these effects resulted from both sensory and motor mechanisms (Dyhre-Poulsen, 1978; Coquery, 1978). Active exploratory hand movements were noted to lead to enhanced perceptual discrimination, i.e. when the subject purposefully tries to extract information from an unknown tactile environment. In this situation all the tactile sensations may be considered to be unexpected. Therefore, it was especially interesting that studies of high-level somatosensory processing in monkeys showed single unit responses that were *attenuated* when the tactile stimulation followed

encounters with familiar, expected, surfaces, and that the cells hence seemed to selectively code unexpected tactile sensations.

Expectation can also result from previous experience either in a specific experimental condition or in a naturally occurring situations whence externally-induced stimuli can be expected as well. Natural situations provide ample examples where environmental events lead to expectations and it has been suggested that the mechanisms may even be hard-wired for those that are biologically important (Bullock, 1988). Several brain areas contain cells which exhibit anticipatory "tactile" responses to the sight of approaching touch (Hyvärinen & Poranen, 1974; Sakata, 1975; Leinonen et al., 1979; Rizzolatti et al., 1981b; Mackay & Crammond, 1987; Mistlin & Perrett 1990) and even though these responses might be reflecting the bimodal response properties of the cells, it is still meaningful to consider their biological function in the context of expectation. The response properties show a complex interaction with the localization of the tactile receptive fields and the localization and direction of visual motion. The anticipatory responses were suggested to be used to prepare the animal for behavioural responses. One class of cells in area STP, however, showed very different behaviour, where the responses to tactile contact were attenuated when the contact was anticipated by witnessing the approaching stimulus (Mistlin & Perrett, 1990). It could be hypothesized that the "anticipatory" tactile responses from parietal cortex are "matched" with the exafferent tactile input. Certain STP neurons could compare the actual tactile input to the existing expectation (which might take a form of a neural template, cf. Freeman, 1979 in section 2.6) and if they match, they cancel each other. Thus the STP cells which show the effects of "expectation" would be either units performing the comparison or, more likely, cells representing an output stage from this matching mechanism. Experimental results seem to give general support for the existence of such matching mechanisms. Hocherman et al. (1981) suggested two such mechanisms: a signal-match and an error-detection mechanism. Neurons belonging to the first mechanism

become activated when the actual input signal matches with the expected one, whereas the cells in the latter group signal unexpected stimulation.

Before any neurophysiological studies had been carried out from the dorsal bank of the anterior STS, Jones and Powell (1970) discussed the possible functional roles of this area especially in the context of higher cognitive functions. This discussion was based on the finding that visual, somatosensory and auditory systems all converge in the upper two-thirds of the superior temporal sulcus. Since those early days the anatomical convergence of different sensory systems as well as the convergence of the visual pathways for object recognition and object location/motion in this area has been repeatedly established (Mesulam et al., 1977; Seltzer & Pandya, 1978, 1984; Neal et al., 1988; Zeki & Shipp, 1988; Boussaoud et al., 1990; Morel & Bullier, 1990; Baizer et al., 1991) and supported by the data from functional studies based on single cell recordings (Benevento et al., 1977; Desimone & Gross, 1979; Bruce et al., 1981; Perrett et al., 1985b, 1989b,c, 1990a, b; Baylis et al., 1987; Mistlin & Perrett, 1990). and lesion studies (Petrides & Iversen, 1979; Luh et al., 1986).

The convergence of different sensory-related inputs in a given cortical zone may allow for intermodal exchange of information. Within STP this kind of intermodal exchange of information has been shown to be present at the level of single cell function (Benevento et al., 1977; Bruce et al., 1981; Mistlin & Perrett, 1990). In somatosensory processing the STP cells have access to a great deal of information concerning the tactile properties of surfaces in the environment, their location, the position and trajectory of animal's limbs etc. In the visual modality it was shown that STP is a site of convergence for the "form" and "motion" processing systems. According to the functional organization of visual areas presented by Felleman and Van Essen (1991) the shortest route to relay form information to the anterior STP would be $V1_{(P)} - V4 - CIT - AIT - STPa$, whereas motion information would follow $V1_{(M)} - MT - MST - STPp - STPa$. Studies by Perrett et al. (1985b,

1989b,c, 1990a,b) have provided neurophysiological evidence for this convergence by showing that area STPa contains cells which are selective for both the sight of a body (form) and moving in a certain direction (motion).

In addition, as a high level cortical association area and through its connections with inferotemporal cortex, amygdala and hippocampus, the STP is likely to be involved in visual mnemonic functions as well. Now, a brain area like STP which is provided with multimodal information from the environment seems to be especially suitable for functioning as an "attentional" gate for behavioural response mechanisms. Interestingly, it has been suggested that the function of the head view selective cells in the STP might be, not form processing as such, but in coding the direction of attention of other individuals (Perrett et al., 1992). These functions may very well be closely linked with the attentional control of the perceiving individual itself.

Mistlin and Perrett (1990) remarked that the apparent lack of selectivity for the nature of the tactile stimuli when studied in anaesthetized animals was surprising given the high-level stimulus selectivity present in visual processing within this same area. By recording from awake animals they found that the cells seemed to code the expectation of the tactile stimuli rather than any simple physical stimulus features as such. As the area is mainly concerned in processing visual information the question naturally comes to mind, is it possible to find similar effects of expectation within visual processing within STP? The following anecdotal observation revealed accidentally that this might be the case.

As noted above, among the highly selective cells for body movements, area STP also contains neurons responsive to movement but lacking any kind of apparent selectivity for form (Bruce et al., 1981; Perrett et al., 1985b; Baylis et al., 1987). In one occasion of recording, one such a cell was found to be very sensitive for the

smallest movements anywhere in the monkey's visual field, regardless of the direction of the movement or the visual qualities of the moving stimulus. Surprisingly, when the monkey was allowed to reach out from the primate chair and move its arm and hand in view, the cell sustained its level of spontaneous activity. In this situation the monkey's hand motion could be classified as expected. This observation initiated the series of present experiments. The experimental work described in the following chapters was designed to investigate whether the visual motion processing in area STP is affected by the operation of high-level expectations and how the visual motion processing interacts with simultaneous motor activity or sensory processing in another sensory modality.

CHAPTER 5

GENERAL METHODS FOR THE EXPERIMENTS

5.1. SUBJECTS AND TRAINING

The subjects used for the neurophysiological experiments were juvenile macaque monkeys (*Macaca mulatta*). The training usually started when the subjects were about 30-36 months of age at which time they weighed around 3-4 kg. The first stage of the training was to get the monkeys to climb voluntarily into a primate chair and sit there quietly. Their access to water in their home cages was restricted to certain periods of the day. Soon after they had adapted to sit in the primate chair, a pair of licktubes was introduced into the chair in front of the monkey's mouth. The licktubes were connected to a solenoid driven pump system which was activated by closing a circuit between the chair and the licktubes, i.e. when the monkey touched the licktubes with its tongue. As the monkeys were restricted from access to water in their home cages they learnt quite quickly to lick the tubes in order to get liquid. Sweet blackcurrant juice was used as the monkeys were observed to prefer its taste. These first training sessions lasted usually from 30 to 60 minutes after which the monkey was returned to its home cage.

At the second stage of the training the monkeys were trained to direct their attention to a small LED light spot on a large white screen at a distance of 4 meters in front of them. The LED was located directly in front of the monkey, approximately at eye level. This training was started by restricting the originally unlimited supply of juice from the licktubes. Now, the monkey could activate the pumps only during a period of time after a short tone signal while an LED light spot of green colour was

illuminated. First, relatively long periods of LED illumination were used. As the monkey began to associate the illumination of the green LED with the possibility for juice, an LED of red colour was gradually introduced. If the monkey activated the pumps by licking the tubes during a red LED illumination, the tubes delivered mildly aversive weak saline solution instead of sweet juice. As the training progressed, the proportion of red LED presentations was increased towards 50% of the trials and the period of LED illumination was shortened towards one second.

At the final stage of the basic behavioural task there were five LEDs on the screen. The central one located directly in front of the monkey at eye level. Two lateral LEDs were located at the same level, 15 degrees of visual angle to left and right from the central fixation point. Another pair of vertically aligned LEDs were located 10 degrees of visual angle above and below the central fixation point. The sequence of events during a trial was as follows: a) a trial started with a delivery of a 500 ms warning tone signal, b) this was followed by a presentation of either a green or red LED light for 1.0 s (the colour of the LED lights was changed in random order across trials, controlled by a computer program), and c) behavioural response by the monkey. The correct behavioural response on trials with a green LED was a lick of a tube for fruit juice reward and the latency for this response was measured. Lick responses to the red LED were discouraged with the delivery of a weak saline solution and, therefore, a correct behavioural response on these trials was to withhold the lick response. The monkeys performed the LED colour discrimination task at a high level of accuracy (>90%, reaction time = 300-500 ms). When the initial training was completed the subjects were ready to be operated for the neurophysiological experiments. One monkey was further trained to perform in a special task. The details of this task will be described together with the experimental results in Chapter 8.

5.2. SURGICAL PROCEDURES

Before the actual operation an implant frame containing two stainless steel recording wells (16 mm internal diameter, ID) and two plastic tubes (5 mm ID) was constructed. A plan view of the implant was drawn on a graph paper. The centers of the wells were located 12-15 mm to the left and right of the implant midline. In the antero-posterior direction the centers of the wells were 3-7 mm apart from each other, the left well being usually the more anterior one. The two plastic tubes were located perpendicularly to the midline of the implant so that the distance between the centers of the tubes was approximately 65 mm. For the implant construction a plan view drawing was covered with a sheet of glass and the wells and plastic tubes were positioned on their correct places. These four separate pieces were connected together by constructing a frame from dental acrylate (Autenal Dental Products Ltd, Harrow, England). Small quantities of liquid dental acrylate were gradually applied on the sheet of glass to form a thin rim around the bases of the wells and a cross-shaped ridge connecting the wells and plastic tubes together. After the dental acrylate had hardened, the implant was strong enough to be removed from the glass plate. Applying a small amount of water helped break the temporary seal between the implant and glass.

A day before the surgical operation took place the monkey was restricted from water and food. On the morning of the operation day an injection of atropine (1 ml i.m.) was administered to the monkey and it was sedated with a weight-dependent dose of intramuscular ketamine and anaesthetized with intravenous barbiturate (Sagatal). The monkey was positioned in a stereotaxic apparatus with its head fixed to a stereotaxic frame (David Kopf). Full sterile precautions were employed during the operation. The monkey's breathing rate was monitored every 30 minutes. This and any sign of stretch reflexes were used to monitor the depth of the anaesthesia.

The operation was started by making an incision to the scalp in an antero-posterior direction. The skull was exposed and cleaned. The previously prepared implant frame was attached to the stereotaxic apparatus and lowered onto the bone of the skull so that the centers of the wells were positioned around the level of 10 mm anterior to the interaural plane. The edges of the wells were drawn on the bone with a China graph pencil after which the implant frame was raised up again and removed from the stereotaxic apparatus. After this a craniotomy was performed. Two round-shaped pieces of bone were carefully cut out by using an electric drill. The exposed dura was left intact. After the craniotomy, the implant was again fixed to the stereotaxic apparatus, adjusted to its correct position and lowered onto the skull. Several (6-8) small elongated holes (6x2 mm) were drilled into the skull. Small H-shaped pieces of stainless steel were fitted into these holes through the skull in order to secure the implantation. In addition, stainless steel screws were screwed to the skull to surround the implant and a steel wire was fixed around these screws to give extra support for the final implant. After this, liquid dental acrylate was gradually applied on the top of the skull to cover the implant frame and to form a mass of acrylate covering the whole top of the head.

Following the operation antibiotics were administered to the animal and it was returned to its home cage. An electric blanket was used to maintain a constant body temperature. The monkeys gained their consciousness within two hours and they were fully mobile on the following day.

5.3. SINGLE-UNIT AND EYE MOVEMENT RECORDING

Two weeks after the implantation the subjects were seated in the primate chair and retrained to perform in the behavioural task for 1-4hrs. Now, the monkey's head was restrained with two metal rods by passing them through the plastic tubes in the

implant. After the monkey had reached the pre-operative level of performance in the color discrimination task, the recordings were started.

For each recording session topical anaesthetic, lignocaine hydrochloride (Xylocaine 40 mg/ml) was applied to the dura and a David Kopf micro-positioner was fixed to the recording well. A trans-dural guide tube (outer diameter, OD, 1.0 mm) was inserted 3 - 5 mm through the dura and a tungsten in glass microelectrode (OD 0.5 mm, Merrill & Ainsworth, 1972) was advanced with a manual or hydraulic micro-drive to the target area in the temporal lobe. These procedures allowed recordings to be made repeatedly (over periods of up to 2 years) without intracranial infection. The target area for recording was the anterior part of the upper bank of the superior temporal sulcus (areas TPO and PGa of Selzer & Pandya, 1978).

The horizontal and vertical eye position was monitored and recorded by using an infra-red corneal reflection system (ACS) adapted to allow recording of both signals from one eye. At the beginning of each recording session the eye-movement recording system was calibrated by requiring the monkey to perform the red/green colour discrimination task with each of the five LED locations on the screen. Over the central field of view (± 15 degrees), this simple calibration procedure achieved an accuracy of ± 2.0 degrees from such trials which was adequate for the purposes of this study.

5.4. DATA COLLECTION AND GENERAL TESTING PROCEDURE

Single cell activity was amplified (Neurolog NL 104), filtered with a 50 Hz filter together with low-pass (800 Hz) and high-pass (20 kHz) filters (Neurolog NL125), monitored with an oscilloscope and an audiomonitor, converted to TTL pulses by a spike processor (Digitimer DM130), and sampled with an AT compatible PC

microcomputer every 5 ms (Hyundai 286 or Dell 386). The horizontal and vertical eye position signals were filtered, digitized every 5 ms, and stored together with the single unit activity on the computer hard disc.

After isolating a cell by spike wave form and amplitude its responsivity to visual stimuli was initially tested using a 20 cm square liquid crystal shutter (Screen Print Technology Ltd., rise time < 15 ms) placed 15 cm in front of the monkey's eyes. On each trial 3D stimuli were presented from behind the shutter which became transparent for 1.0 s, after a 0.5 s signal tone. It otherwise remained opaque white. The central fixation LED was also visible during the period the shutter was open. Cells were also tested with projected 2D stimuli. The stimuli were stored on a laser video disc (RLV Mk II, Optical Disc Corp.), replayed with a video disc player (Philips VP406 LaserVision Disc Drive) and projected onto the screen on which the LEDs were located (using a Sony colour video projector VPH-1041QM). The testing involved computer controlled selection of desired stimuli and "unblinking" (switching on with 0 ms delay) the video signal to the projector for a 1 s stimulus presentation. The details of the specific tests used in the experiments will be described in each experimental chapter.

5.5. PERFUSION AND HISTOLOGY

Following the last recording session, the animal was prepared for the perfusion. The monkey was given a sedating dose of ketamine followed by a lethal dose of barbiturate anaesthetic. Once deep coma had been reached, the animal's thorax was opened to reveal the heart. The pericardium was carefully cut away to reveal the heart. A small puncture was made in the left ventricle and a large bore cannula inserted. The descending aorta was clamped in order to speed up the perfusion of the

brain. The right atrium was also punctured to allow the exit of the blood/pre-fixative wash. As the animal was in deep coma the heart was still beating.

After the cannula placement the pre-fixative wash, phosphate buffered saline + 0.2% NaNO₃ (for vasodilation), pre-warmed to 37 degrees centigrade was passed through the animal. A mechanical centrifugal pump was used to assist the pumping of the heart. Approximately 5 litres of the pre-fixative wash was pumped through the animal until there was little or no blood coming out in the pre-fixative wash.

The perfusing fluid was then changed to the fixative. A phosphate buffered fixative (4% paraformaldehyde, 0.5% glutaraldehyde) was used. The fixative was used until the muscles of the neck and face went rigid. Approximately 5 litres of fixative was used. Once full rigidity of the muscles of the head and neck had been achieved, the fixing process was complete and the cannula removed from the heart. The head was removed from the body and the outer tissue from the skull with a bone scraper. The intact skull was sunk in phosphate buffered fixative to wait for the craniotomy.

Bone cutters were used to open the cranium and reveal the top, back and sides of the cerebrum. The dural tissue was left intact and surrounding the brain as much as possible. Before the brain was removed from the skull 8 vertical stereotaxic injections of cresyl violet were made at -5, +5, +15 and +25 mm relative to the interaural plane, 10 mm lateral from the midline in both hemispheres. In addition, 8 horizontal injections were made, at 5 and 15 mm lateral from the midline at a height of 10 and 20 mm above the interaural plane in both hemispheres.

After the brain was removed from the skull, it was sunk in successively higher concentrations (10, 20 and 30%) of sucrose solution or (5, 10 and 20%) of glycerol and 2% dimethylsulphoxide (Rosene et al., 1986). Immediately before microtome

sectioning the brain was frozen quickly by immersing it into a bath of isopentane which was cooled down to -75°C . with dry ice (CO_2).

A freezing microtome (Bright Instruments Company Ltd, Huntingdon, England) was used for the brain sectioning. The temperature was kept at -30°C . Coronal sections (25 or 50 micron thick) were collected every 0.25 or 0.5 mm which were subjected to routine histological procedures. During microtome sectioning slide photographs were taken of the brain surface every 0.25 mm.

5.6. RECONSTRUCTION OF THE CELL LOCATION

Frontal and lateral X-radiographs were taken of the position of the microelectrode at the end of each recording session. The position and angle of electrode penetration was achieved by measuring the (horizontal) distance of the electrode at two different levels from the midline (frontal view) and from the interaural plane (lateral view). The final depth of the electrode was measured in reference to the horizontal interaural level. These measurements were fed to a computer program which reconstructed a three-dimensional position of the electrode *within the skull*.

Reconstruction of electrode position *in the brain* was achieved by reference to the positions of micro-lesions (10 microamp DC for 30 s) made at the end of some of the last electrode tracks. In one case the electrode position was achieved with micro-injections of Indian Ink made at the site of 4 previous recording tracks where typical STS cell responses were recorded. The photographic slides of the brain surface taken during the microtome sectioning were projected at suitable magnification on the wall and the grey matter boundary was recorded on paper. The photographic record improved the reconstruction accuracy because it was not subject to distortion of the tissue during mounting. The position of the lesioning electrodes and injection

cannulae in the brain tissue was defined by visual inspection of the location of the micro-lesions or injections. The position of the recording electrodes in the brain was defined by relating their X-radiograph measurements to those obtained from the lesioning electrodes and injection cannulae. Finally, as the final depth of the electrode in each track was measured from the X-radiographs the location of the recorded units in the brain was defined by subtracting the depth of the unit from the electrode's final depth as read from the scale on the micro-drive.

CHAPTER SIX

GENERAL RESPONSE PROPERTIES OF MOTION SENSITIVE NEURONS IN AREA STP

6.1. INTRODUCTION

In the macaque monkey the cortical processing of visual motion information involves a hierarchical series of steps through magnocellular layers of the lateral geniculate nucleus, the layers 4Ca and 4B of area V1, the thick stripes of area V2, the middle temporal area (MT or V5), the medial superior temporal area (MST) and an area on the floor of the superior temporal sulcus (FST) (Livingstone & Hubel, 1987; Zeki & Shipp, 1988; Felleman & Van Essen, 1991). After two decades of extensive studies, a considerable body of knowledge has been gathered about the functions of areas MT and MST in motion processing (e.g. Dubner & Zeki, 1971; Zeki, 1974; Ungerleider & Mishkin, 1979; Van Essen et al., 1981; Maunsell & Van Essen, 1983a; Albright et al., 1984; Desimone & Ungerleider, 1986; Tanaka et al., 1986; Saito et al., 1986; Tanaka & Saito, 1989; Sugita et al., 1990; Roy & Wurtz, 1990; Duffy & Wurtz, 1991a,b; Sugita & Tanaka, 1991).

The functional properties of areas MT and MST have already been described in detail in Chapters 2 and 3 and will not, therefore, be repeated here. Briefly, a functional differentiation has been suggested for these areas. Area MT and the ventral part of area MST (MSTv) has been proposed to analyse object-motion characteristics from the retinal image, whilst neurons in the dorsal part of area MST (MSTd) respond to whole-field motion and, therefore, it has been seen to be particularly suitable in analysing visual consequences of the animal's own locomotor activity (Saito et al., 1986; Tanaka et al., 1986; Tanaka & Saito, 1989; Roy & Wurtz, 1990; Saito, 1992).

The motion processing pathway, however, does not "end up" in area FST. As reviewed in Chapter 3, anterior to areas MST and FST in the upper bank of the superior temporal sulcus lies a polymodal area, area STP (superior temporal polysensory area) which receives inputs not only from visual, but also from auditory and somatosensory systems. This elongated brain area receives a direct projection from areas MST and FST (Boussaoud et al., 1990). Supporting the anatomical evidence, a few neurophysiological studies have confirmed that area STP contains units especially sensitive to stimulus motion (Bruce et al., 1981, Perrett et al., 1985b; Baylis et al., 1987; Hikosaka et al., 1988; Mistlin & Perrett, 1990). About half of the units exhibit directionally selective responses. Generally, however, except for the increased receptive field size and occurrence of pandirectional movement sensitive cells, the observed response properties do not seem to suggest any major difference in visual motion processing between areas MST/FST and STP (Bruce et al., 1981; Perrett et al., 1985b; Saito et al., 1986; Tanaka et al., 1986; Hikosaka et al., 1988). The majority of the motion sensitive units in area STP, as in area MST, do not show any selectivity for form, but respond equally well to moving bars, patterns, junk objects etc (Bruce et al., 1981; Perrett et al., 1985b; Hikosaka et al., 1988).

The present chapter will attempt to provide a more detailed description of the general response properties of the motion sensitive, form insensitive neurons in the anterior parts of area STP than has been available before. This task will fulfill two aims. First, it is hoped that by studying the response properties of this particular cell population (e.g. directional selectivity and distribution of preferred directions) a better understanding of the functional significance of area STP in visual motion processing will be achieved. Second, such descriptions will provide the necessary groundwork on which the contents of the following three chapters, the main contribution of this thesis, will rest.

6.2. METHODS

Testing procedure. Before beginning recording the subjects were trained to discriminate between the red or green colour of an LED light as described in Chapter 5. Each cell recorded was first subjected to exploratory testing involving the presentation of a variety of static and moving objects.

The cells were routinely tested for six different directions of movement along 3 orthogonal axes (towards, away, up, down, right, left). This testing included moving several 3D objects in front of the monkey in the preferred direction(s). These objects included various laboratory objects of different shape, size, colour and texture (human faces and bodies, fruit, tools, boxes, fur etc.). Some cells were tested with moving 2D stimuli. These included simple geometrical images (bars, spots, gratings) as well as complex images of bodies. If the cell was observed to respond equally to all stimuli tested in the preferred direction(s) it was classified as a non-form, motion sensitive cell. In some cases the size of the object was found to have an effect on the responses, but as no other selectivity for features could be established, these cells were also classified as form non-selective.

A number of cells lacking form sensitivity but which showed any tendency to discriminate between moving and static objects were then tested with 5 trials of four or eight directions of movement presented in a computer controlled and randomized order. Testing was performed in one mode using either real 3D or projected video film stimuli. 3D test stimuli were presented through a liquid crystal shutter as described in Chapter 5. The stimuli were presented in front or to either side of the LED. In this way the monkey's attention was directed towards the experimental stimuli. The 2D video film stimuli were projected onto the wall on which the LED was located. The monkeys performed the task at a high level of accuracy and independent of simultaneously presented 2D test stimuli.

Recording procedures and data analysis. Extracellular single unit activity was recorded from macaque monkeys (*Macaca mulatta*) using standard chronic recording techniques as described in Chapter 5. Two female (wt 4 Kg) and three male (wt 5-8 Kg) rhesus macaque monkeys were used. The monkeys are referred to as B, F, D, H and J.

Neuronal firing rates were measured using standard techniques in a period of 250 ms beginning 100 ms after stimulus presentation. [This analysis period was selected because most cells in STP have latencies of 100-150 ms. A 500 ms sample period was occasionally used for cells with small or late responses.] These data were analysed on-line by a microcomputer. Horizontal and vertical eye movements were monitored to determine whether any response differences reflected differential patterns of fixation.

Cell responses to 4 or 8 directions, static controls and spontaneous activity were compared on line using 1-way ANOVA and post-hoc tests (protected least significant difference PLSD, Snedecor and Cochran 1980). For cells tested with eight directions multiple linear regression analysis was used to estimate the best relationship between response and 2nd order cardioid function of direction. In effect this calculates the values of the coefficients β_{1-5} of the equation below which produce the highest correlation between response and the angle of motion.

$$R = \beta_1 + \beta_2 \cos \theta + \beta_3 \sin \theta + \beta_4 \cos 2\theta + \beta_5 \sin 2\theta,$$

[Where R is the response, θ is the directional angle and β_{1-5} are coefficients.] This equation was chosen because it makes very few assumptions about the nature of direction tuning. At the outset of the investigation only two types of direction tuning were expected to be encountered; cells with a single preferred direction and cells with two preferred directions approximately 180° apart (e.g. movement left and right).

Where the regression analysis produced a significant ($p < 0.05$) relation between predicted and observed values, the regression equation was used to define:- (a) the optimal direction (θ_{max}), (b) the maximum response at this direction (R_{max}), (c) the sharpness of tuning (average angle of rotation required to reduce the response to half R_{max}) and (d) the angle and magnitude of any second peak in the direction tuning.

After each recording track, frontal and lateral X-radiographs were taken to allow the position of the metal microelectrode to be reconstructed from subsequent histology. The histological procedures were as described in Chapter 5.

6.3. RESULTS

6.3.1. Cell classification

The total number of recorded cells in the STS was 7983 out of which 2208 (28%) were classified as having visually driven responses. 553 of these cells were classified as lacking selectivity for stimulus form but having sensitivity for motion. This is 25.0% of visual cells. Even though auditory and tactile responses were not systematically studied such responses were occasionally encountered. 3.7% and 2.5% of the cells were classified as having tactile and auditory responses, respectively. 65.8% of the cells remained unclassified. However, it is likely that this large class of cells contained cells having auditory and tactile responses if studied more thoroughly.

Cells were screened to check that the response differences to different stimuli were not be due to differences in eye position or movements. No relation was observed between responses and eye movements for any of the cells. Figure 6.1 gives an example of eye position recordings during an effective (moving) stimulus and ineffective (static) stimulus. Recordings show the monkey fixating the position of the

coloured LED before stimulus onset (0 ms), and maintaining fixation for at least a further 200 ms. With the stimuli moving to the left, the cell responded at a latency of

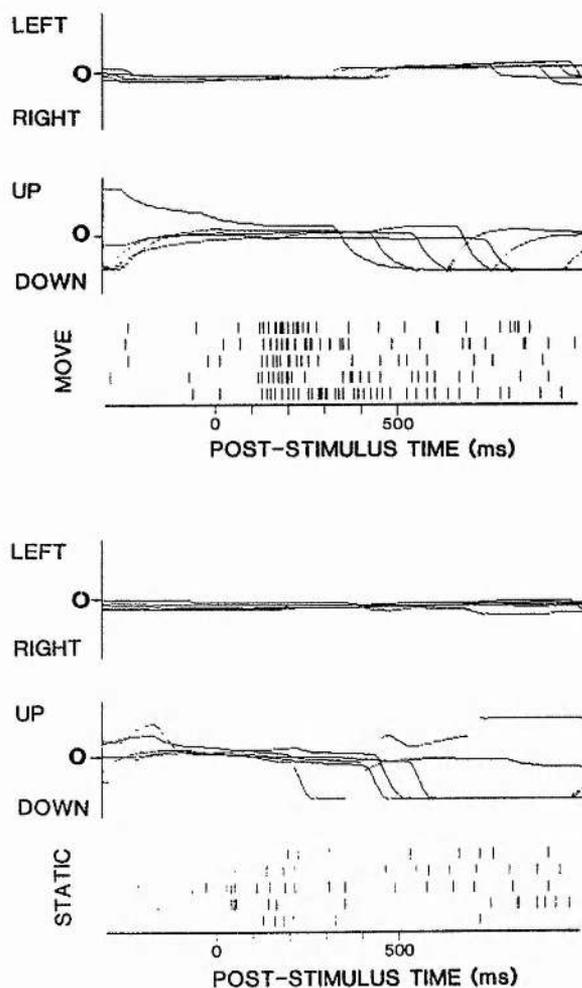


Figure 6.1. Eye movements during effective and non-effective stimulus presentation. Upper: eye position and responses of one cell (J33_25.85) to 5 presentations of an effective stimulus. For this cell movement to the subject's left in the lower half of the visual field elicited a good response (At the onset of trials the subject fixated a centrally positioned LED to determine its colour. Later in the trial the subject made saccades down to the stimulus). Lower: eye position and cell responses to 5 trials of the same object presented stationary in the lower half of the visual field. The eye movements are comparable for both stimuli, yet only when the stimulus was moving was there a cell response. The ordinate axis in the eye position recordings give a scale for ± 20 degrees.

110-130 ms regardless of the latency and pattern of subsequent eye movement. The pattern of eye movements elicited to static stimuli was similar, yet the neural response was abolished. In addition, the cell was also tested with movements to the right and

towards the subject (not shown in Figure 6.1). These directions of motion produced different patterns of eye movement but similar neuronal responses.

As mentioned above, all the cells were routinely tested for six different directions of movement along 3 orthogonal axes. If a cell was found responding preferentially in only one of these directions it was classified as a *unidirectional* cell. Based on the routine screening testing, Table 6.1. presents the distribution of the preferred directions of unidirectional cells recorded from all five subjects. 216/553 (39%) non-form selective motion sensitive cells were classified as unidirectional. *Bidirectional* cells were classified as cells which showed roughly equal responses to two directions 180 degrees apart with responses in orthogonal directions being substantially weaker. 23/553 (4%) non-form selective motion sensitive cells were classified as bidirectional. Finally, the remaining cells showed approximately equal responses to motion in many or all directions and were classified as *pandirectional* (314/553 or 57%).

		Directions						Total
		U	D	R	L	+	-	
Subjects	B	1	3	10	10	4	8	36
	F	26	13	4	0	39	13	95
	D	6	7	9	6	15	5	48
	H	1	1	0	0	2	0	4
	J	7	5	1	7	9	4	33
	Total	41	29	24	23	69	30	216

Table 6.1. The distribution of the preferred directions of unidirectional cells recorded from all five subjects (B, F, D, H and J). The direction of motion is indicated by the symbols: U and D (motion up and down), R and L (motion right and left), + and - (motion towards and away).

After initial directionality screening the directionality of 43 cells was tested with 8 directions of motion in a given plane. (4 cells were tested twice in the same plane to investigate reliability of estimates of directional tuning and 9 cells were

tested in two planes. Of the total of 56 regression analyses 50 (89%) were found to give a significant relation between the response and the second order cardioid function of the direction of movement. 19, 18 and 9 cells with a significant response-direction relationship were studied in the horizontal, fronto-parallel and sagittal planes respectively.

The responses of 32 of the direction selective cells followed a *unimodal* pattern (unidirectional cells), with one direction evoking the optimal response. An example of a unimodal or unidirectional cell is given in Figure 6.2. For this cell, movement with a downward directional component elicited a strong response, whereas movement to either side of the subject or upwards produced responses no different from spontaneous activity (S.A.).

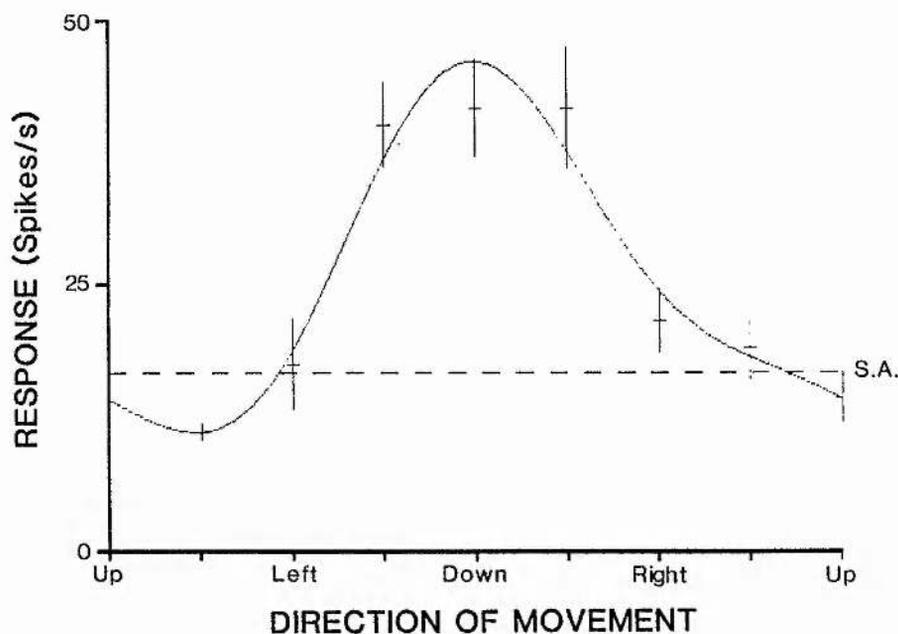


Figure 6.2. Responses of a unidirectional direction-selective cell. The mean responses (± 1 SE) are illustrated for one cell (J68_29,25) to 8 directions in the fronto-parallel plane. Direction is expressed as the angle of rotation from upwards (0=up, 90=left, 180=down, 270=right). The curve is the best fit cardioid function, relating response to direction of motion ($R^2=0.675$, $F_{4,35}=18.2$, $p<0.0005$). The dashed line denotes spontaneous activity (S.A.). Responses to movement downwards (down and left, down and right and straight down) were significantly greater than movements in other directions and S.A. (PLSD, $p<0.005$ each comparison), but were themselves equivalent ($p>0.75$). (ANOVA, $F_{8,36}=10.6$, $p<0.0005$).

5 direction-selective cells were classified as bidirectional because their responses to two directions were both significantly ($p < 0.05$) higher than intervening directions. Figure 6.3. shows responses of a bidirectional cell selective for motion to the subject's left and right. For all bidirectional cells in this study the two preferred directions were approximately 180° apart. The criterion for classification as bidirectional used here was fairly stringent and a further 3 cells showed a degree of bidirectional direction tuning, in that their response to a second or minor direction was greater than half the response to the optimal direction (with other intervening directions evoking less than half the maximal responses).

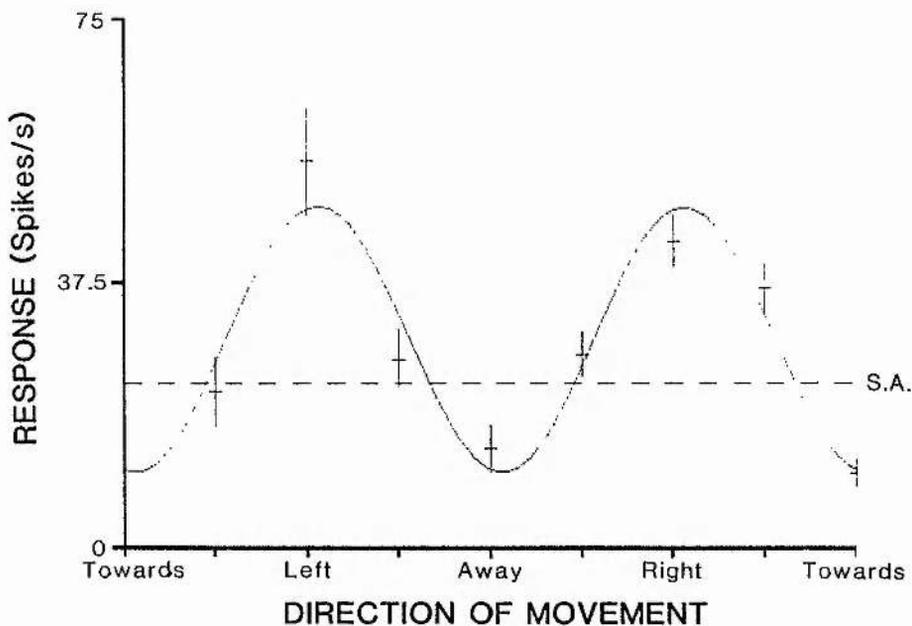


Figure 6.3. The responses of a bidirectional direction-selective cell. Responses (mean \pm 1 SE) of a cell (D58_30.78) to 8 directions in the horizontal plane. Direction is expressed as degrees of rotation away from movement towards the subject (0° =towards, 90° =left, 180° =away, 270° =right). The curve is the best fit cardioid function, relating response to direction of motion ($R^2=0.604$; $F_{4,43}=16.5$, $p < 0.0005$). The dashed line represents spontaneous activity (S.A.). The cell responded to movements left or right more strongly than to movements towards or away from the subject ($p < 0.0005$ each comparison). The responses to movements left and right were statistically indistinguishable ($p=0.09$). (ANOVA, $F_{8,45}=9.1$, $p < 0.0005$).

As already noted, more than half (57%) of non-form selective motion sensitive cells recorded were responsive to movement of an object in many or all directions. Some of these cells (e.g. Fig. 6.4) also exhibited weak directional selectivity. For the

cell illustrated in Figure 6.4 movement of an object in any direction in the fronto-parallel plane caused the cell to respond, whereas the same object held stationary elicited no response. The responses to all movements were not equivalent, however, in that movement to the subject's left and downwards gave a significantly greater response than movement upwards.

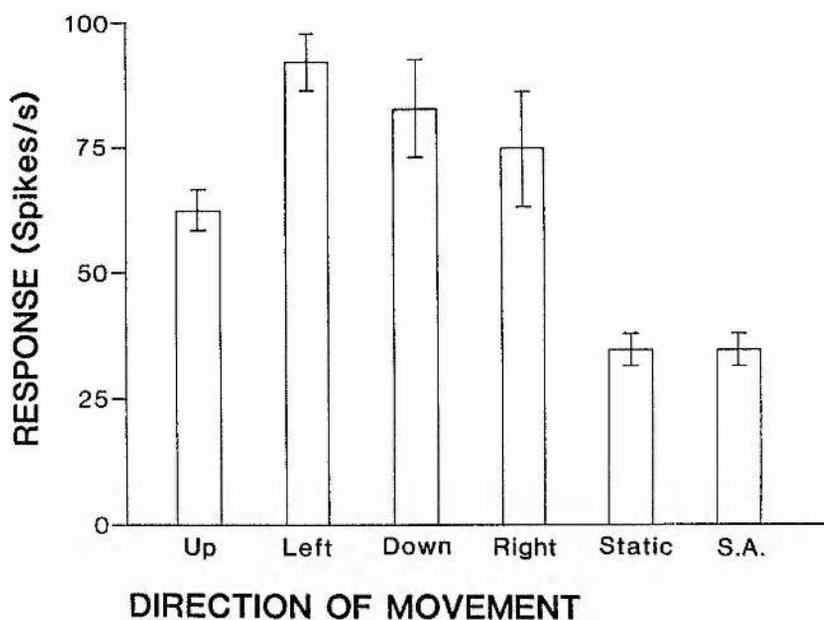


Figure 6.4. The responses of a cell responsive to multiple directions of motion. Responses of a cell (J131_26.11) to 4 directions in the fronto-parallel plane. Movement in any of the tested directions gave a response that was greater than spontaneous activity (S.A.) and static views of the same object ($p < 0.01$ each comparison). The cell responses however showed slight selectivity for direction of movement with a significantly greater response to movement to left and down than movement up ($p < 0.05$). (ANOVA, $F_{5,24} = 12.0$, $p < 0.0005$).

6.3.2. Discrimination between directions

A number of indices have been used to estimate response discrimination between directions of movement. A commonly used direction index is $I_d = 1 - (R_{opp} - S.A.) / (R_{max} - S.A.)$, where R_{opp} is the response magnitude to motion in the opposite, or null, direction to that which gives the maximal response magnitude (R_{max}). This index was calculated for the unidirectional cells. As ANOVA revealed no significant differences between planes for the index ($p = 0.28$) the data for cell testing in different

planes were combined. Figure 6.5 shows the frequency histogram of the discrimination index for 44 cells. A directionality index of 0 indicates no difference in responses to the null or preferred direction, and index values > 1 indicate suppression of activity below spontaneous activity to direction of motion in the null direction. For the 44 directional selective cells the mean value of the directionality index was 1.01 (± 0.04) ranging from 0.39 to 1.65.

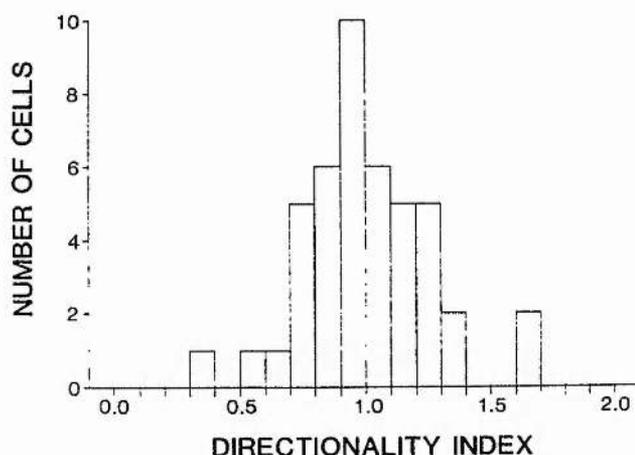


Figure 6.5. Directionality index expressing response discrimination between optimal direction and opposite (null) direction (for details see text).

6.3.3. Width of tuning of direction-selective cells

Width of tuning was calculated as the average angle required to reduce firing rate to half of the difference between response to the most and least effective directions $[(R_{\max} - R_{\min})/2]$ or $1/2$ width at $1/2$ height measure]. As no significant differences were found for cells sensitive to motion in different planes ($p = 0.26$), the estimates from all 3 planes were combined. Figure 6.6 illustrates the width of tuning estimate for all direction-selective cells tested with 8 directions and with significant cardioid regressions (1 value per cell).

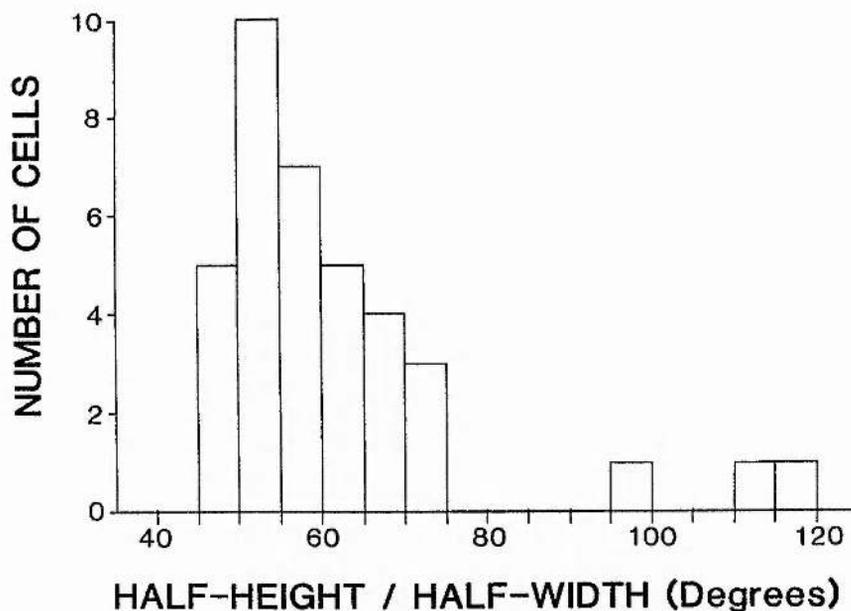


Figure 6.6. Width of tuning. The average angle of rotation required to reduce response by half of difference between response to the most and least effective direction ($(R_{max}-R_{min})/2$) is plotted for 37 direction selective cells.

Half width at half height ranged from 45° to 120° . The distribution of directional tuning in Fig. 6.6 illustrates two important points, first the majority of cells have tuning less than 75° (1/2 width) and second, the distribution does not appear continuous. Using 90 degree 1/2 width tuning as a cut off point 34 cells were defined here as having relatively 'narrow' tuning for direction and 3 cells as having 'broad' tuning

The distribution of width of tuning is skew positive with no cells having 1/2 width $< 45^{\circ}$. This is in part an artifact of regression analysis since the cardioid equation used cannot follow changes in response from maximum to minimum in less than 90° . Therefore for 5 cells, the width of tuning was artificially broad (by an estimated 5-15 degrees). Since this error affected a minority of cells it does not affect estimates of the width of tuning of the cell population unduly.

6.3.4. Average shape of direction tuning

To make a visual comparison across different tuning curves the raw data for each cell was rescaled (so that $R_{max} = 1.0$ and $S/A = 0.0$) and directions expressed as angles of rotation from optimal (Soodak and Simpson 1988). Figure 6.7 illustrates the range of the individual tuning curves for a sample of 29 unidirectional cells with narrow tuning.

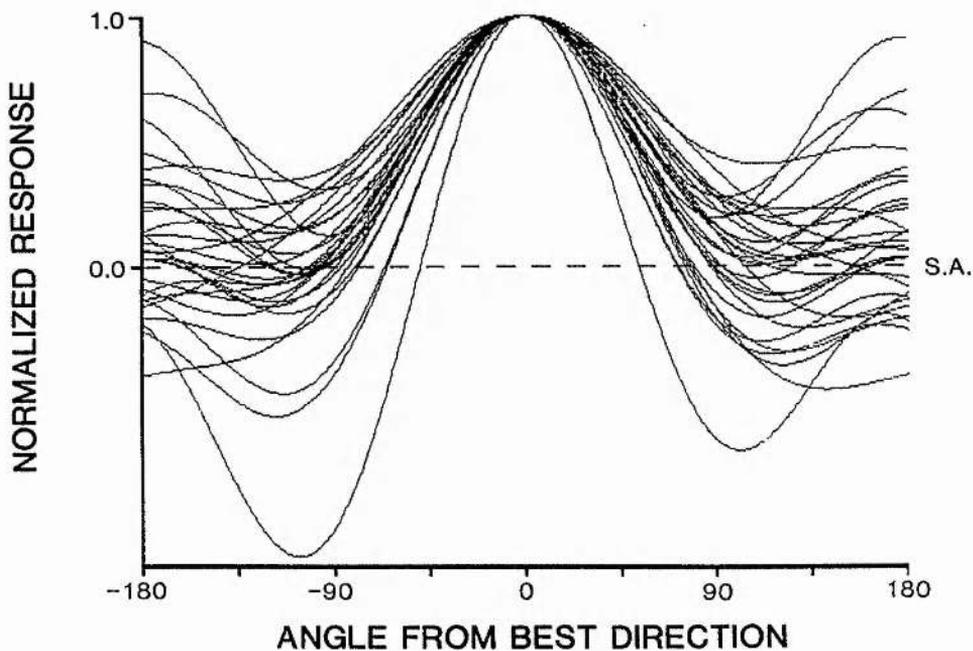


Figure 6.7. Tuning curves of direction-selective cells displaying unidirectional narrow tuning. The tuning curves (estimated from best fit cardioid function relating response to direction of motion) for 29 unidirectional direction-selective cells. Each tuning curve is normalized so that maximum response = 1.0 and spontaneous activity (S.A.) = 0. Direction is expressed as an angle of rotation from optimal direction for each cell (q_{max}).

6.3.5. Distribution of optimal directions

The optimal response directions were analysed for all cells which (a) were tested with 8 directions, (b) displayed a significant ($p < 0.05$) relation between response and a cardioid function of angle of motion (equation 1) and (c) for which Chi-Squared comparisons between predicted and observed response indicated a good fit. Thus data were considered for only those cells for which regression analyses produced appropriate optimal response angles.

Figure 6.8 shows the distribution of the optimal directions from the 46 appropriate analyses. For each cell the optimal direction is represented by a single line. For cells tested twice in the same plane the first estimate of optimal direction is plotted. Where testing was performed in two planes both estimates have been entered in the appropriate Figure. The optimal directions of cells appear clustered around cartesian axes, (up/down, left/right and towards/away). To evaluate this clustering the estimated optimal direction is expressed as the angular rotation from the nearest cartesian axis. Statistical analysis confirms that significantly more cells have optimal directions that are 'on axis' (within 22.5 degrees to a cartesian axis) than would be expected by chance (Binomial Test $p < 0.0005$).

6.3.6. Temporal characteristics of cell responses

The responses of the cells to moving objects showed a fast rising phase to a peak, then a more gradual decay down to an apparently steady firing rate. The steady firing rate (estimated from the final 100 ms of the data collection period of 1 second) was found to be above the spontaneous activity level for all cells.

15 cells were studied where the data had been collected to 5.0 or 5.2 ms accuracy. The spontaneous activity of these motion sensitive cells lacking form selectivity ranged from 0.8 to 40.8 spikes/s (mean 11.4). Response latency varied

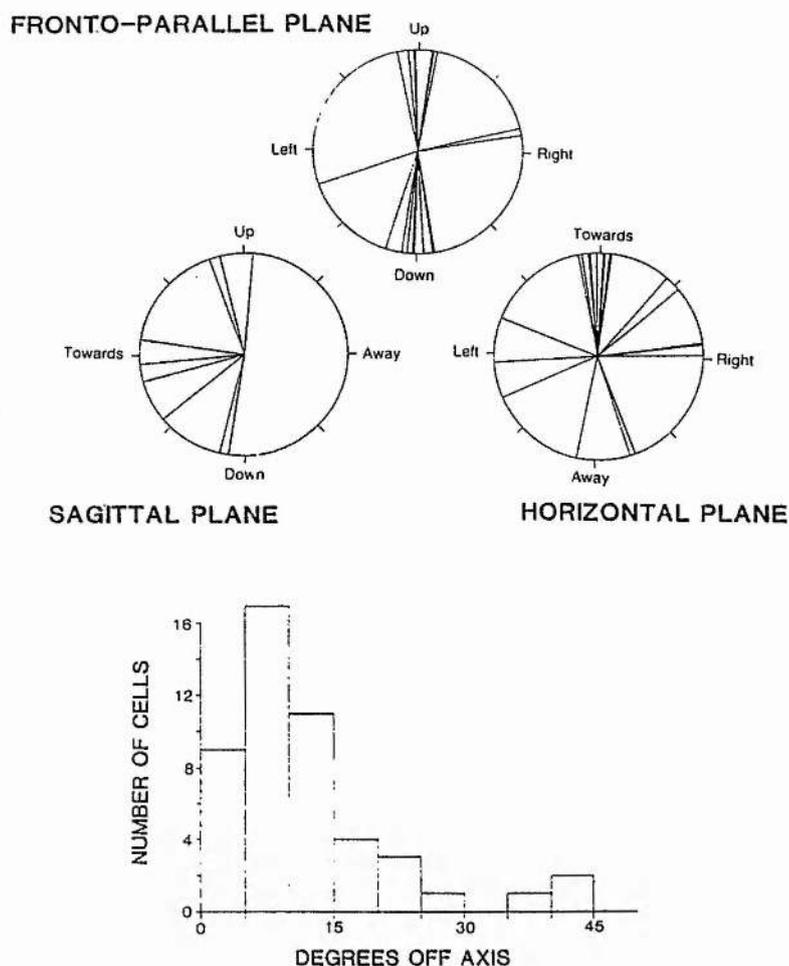


Figure 6.8. The distribution of preferred directions across the population of direction-selective cells. Upper: polar plots with each line representing the direction estimated from regression analysis to evoke maximal response for one cell, plotted separately for horizontal, fronto-parallel plane and sagittal plane. Lower: histogram of the number of cells for a given rotation away from a cartesian axis independent of the plane of testing. Significantly more cells exhibit a preference for directions within 22.5° of cardinal directions (Up, down, left, right, towards and away) than for intermediate directions (44 out of 46, $p < 0.0005$).

between 35.0-126.4 ms (mean 90.9) and the maximum firing reached values between 62.2 and 175.9 spikes/s (mean 108.3).

6.3.7. Location of cells

Histological reconstruction of the positions of cells recorded in monkeys F, B and D indicated that the majority of non-form motion sensitive cells were located in the

cortex of the upper bank of the superior temporal sulcus (areas TPO and PGa of Seltzer & Pandya, 1978). The proportions of cells found sensitive to movement but lacking form selectivity out of the total number recorded within STP varied from subject to subject (B, 10.6% (67/632); D 11.1% (155/1397); F, 14.8 (225/1553); J, 5.5% (88/1613) [N.B. these figures include cells responsive to motion that were not investigated in detail for direction selectivity]. Measurements of the position of recording electrodes (from X-radiographs) indicated cells sensitive to motion but not form in monkeys J and H were recorded in the same region.

Figure 6.9 displays the reconstruction of the position of directionally selective cells that were recorded in the upper bank of the STS in the right hemisphere of one monkey (D). Neighbouring cells on the same track showed a tendency to display similar direction preferences. With the resolution of reconstruction present (± 1.0 mm) there was no obvious anatomical organization (patchiness) of direction coding within the cortex of this monkey. All directions of motion appeared to be coded in the same patch of cortex.

6.4. DISCUSSION

Previous work with STP cells responsive to visual stimuli has focused mainly on coding of information about the form of the stimulus. Indeed the lateral temporal lobe is often considered as containing high level form representations. The current study evaluated coding of direction information where the cell responses had no sensitivity to the form of the stimulus. These cells were found in the same loci as cells selective for static form information (Perrett et al., 1982, 1984, 1985a, 1987, 1989a, 1991, 1992; Baylis et al., 1985; Rolls & Baylis, 1986; Hasselmo et al., 1989). This shows convergence of both form and motion information processing streams in the anterior portions of STP.

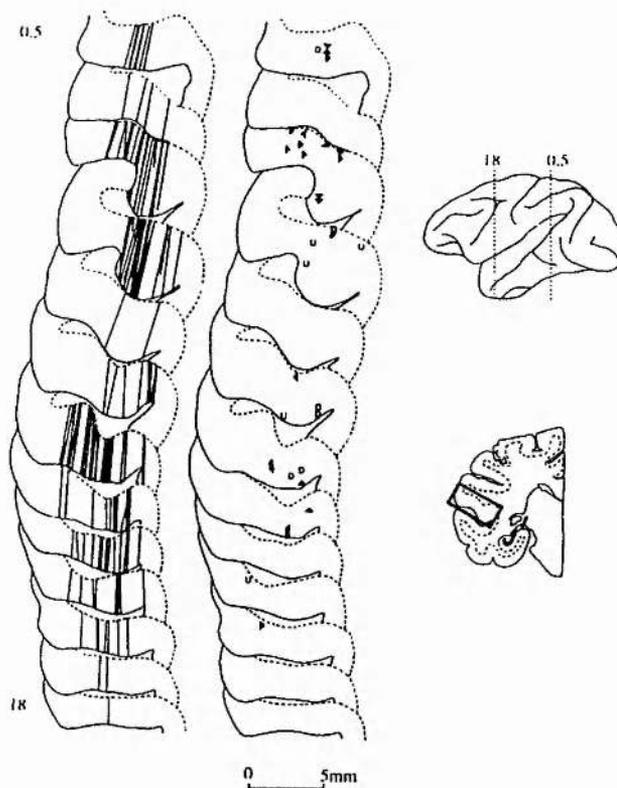


Figure 6.9. Histological reconstruction of position of cells selectively responsive to motion but lacking form sensitivity. Upper right: lateral view of the right hemisphere showing the antero-posterior extent of sampling. Lower right: a coronal section at 3.0 mm posterior to the mid-geniculate level. The box shows the position of the superior temporal sulcus (STS). Left: serial sections (every 1.0 mm) of the upper bank of the STS from 3.0 mm posterior to 9.0 mm anterior to the mid-geniculate level from the right hemisphere of one monkey (D). Vertical lines indicate the position of all recording tracks in this hemisphere. Centre: position of movement sensitive cells. The preferred direction of motion for each identified cell is indicated by the symbols: up and down arrows (motion towards and away), left and right arrows (motion left and right), U and D (motion up and down).

In keeping with the relatively low rate of spontaneous activity, *optimal* directions appeared to be coded by excitation rather than inhibition. A cell could theoretically code the presence of one direction by a selective reduction of response rate below spontaneous activity for that direction, with no change in activity for other directions. No such cells were found. There was however some evidence for suppression of activity to non-preferred directions.

One of the clearest findings of the present study was the prevalence of direction-selective coding clustered around particular axes. These axes correspond to the gravitational axis (up/down), the towards/away axis, and the axis running left/right. The width of the tuning of the cells suggests that coding of these 6

directions is sufficient to allow representation of all possible directions of movement within the STS. Movement at 45 degrees to the cartesian axes would excite (half maximally) at least two cell populations tuned to directions along axes. The preferential coding of orthogonal directions means that all directions in three dimensional space can be represented by the minimum number of directionally selective cell populations. Therefore not only are all directions represented in the STS, but also they are represented in the most efficient manner.

It is of interest to speculate why these particular three axes are represented. If directional tuning is affected by experience then the particular set of axes is not too surprising. The up down axis is of course, co-incident with gravity; thus this axis could be defined through experience of objects falling. Movement towards any organism has strong survival implications, and for social animals, such as macaques and humans, it is a powerful cue to social interactions. From optical considerations objects moving along this z axis will change in retinal size. The presence of retinal expansion/contraction could therefore be used to define the selectivity of cells tuned for movement towards and away.

Relationship of motion selective cells in STP with cells in MT, MST and posterior STP (STPp). In areas MT, MST and STPp, virtually all visual cells (>90%) are non-selective for stimulus form but responsive to motion (Tanaka et al., 1986; Hikosaka et al., 1988; Saito et al., 1986; Duffy & Wurtz, 1991a). This is far above the 25% of the neurons in the anterior portions of STP showing similar properties found in the present study. The major difference between non-form, motion selective cells of STP and MT and MST is in the number of pandirectional as opposed to unidirectional cells. Studies of MT revealed only 2% (Tanaka et al., 1986), of motion selective cells were pandirectional. A similarly low proportion of pandirectional cells was found in MST (Tanaka et al., 1986; Saito et al., 1986). In a third study of MSTd, some 30% of the cells were responsive to rotation, movement in the fronto-parallel plane and

expansion/contraction, but of those tested in the fronto-parallel plane only 7% responded to all 8 directions tested (Duffy & Wurtz, 1991a). All these estimates are far lower than the 56% of motion sensitive cells being pandirectional found in the present study, even if one assumes that the reduction in the proportion of non-form motion selective cells is entirely due to a reduction in unidirectional cells. In STPp however 29.8% of motion sensitive cells are pandirectional (Hikosaka et al., 1988), suggesting that there is a trend from MT/MST to STPp to STPa for the number of pandirectional cells to increase.

The proportion of motion selective cells showing bidirectional properties reported in MT and MST (6% and 1% respectively, Tanaka et al., 1986) is far more comparable to the present study (4%), as is the 3.5% reported for STPp (Hikosaka et al., 1988). Thus the change in proportion of unidirectional to pandirectional cell selectivities seen from MT/MST to STP is due to a drop in the very high proportion of unidirectional motion selective cells in MT and MST (86% and 80% respectively, Tanaka et al., 1986).

Of the unidirectional cells in MT, MST and STPp relatively few respond to expansion or contraction (2.6% in MT, 19% in MST, Tanaka et al., 1986; 13.2% in STPp, Hikosaka et al., 1988). In the present study 46% of unidirectional cells responded to movement towards or away from the monkey. This apparent discrepancy could be due to the differences in methods. In the present study the STPa cells were tested by using 3-D stimuli and expansion/contraction cells in MST have been reported to respond preferentially to real 3-D stimuli over projected stimuli (Tanaka & Saito, 1989). The ratio of unidirectional cells in MSTd responsive to expansion compared to contraction ranges from about 2:1 (Saito et al., 1986) to 76:11 (Tanaka & Saito, 1989). The ratio of the present study was 67:28. Thus in MT, MST and STP there is a higher concentration of cells selective for motion towards the

monkey, but the proportion of cells sensitive to motion towards or away from the monkey is much higher in STPa than in MT, MST or STPp.

Thus the changes that seem to occur between MT, MST, STPp and STPa can be summarised as follows: (1) the proportion of motion sensitive cells decreases, (2) there is a trend for fewer unidirectional cells and more pandirectional cells, (3) the proportion of bidirectional cells stays roughly equivalent indicating that they form a separate population, (4) the proportion of motion sensitive cells preferring motion towards or away from the monkey increases.

Directional tuning in different brain areas. Unlike the cell population studied here, the optimal direction for MT neurons is evenly distributed around the fronto-parallel plane (Albright et al., 1984; Komatsu & Wurtz, 1988a). In MST cells responsive to motion in the horizontal plane show a slight preference for motion towards the ipsilateral side (Komatsu & Wurtz, 1988a).

Duffy and Wurtz (1991a) used a measure that is equivalent to the measure of directionality used in this study (see Fig. 6.5), and in their study of the cells in the dorsal parts of area MST found that 55% of unidirectional cells (including cells selective for rotation) had a value > 5.0 . This corresponds to values > 0.8 in Figure 6.5. In STPa more than 80% of the cells fell in this range. The direction index of cells in areas MT, MST and STP certainly indicates far greater direction discrimination than estimates for V1 directional cells (Snowden et al., 1992).

The range of the width of tuning as measured by 1/2 height 1/2 width measure in the present study was 45 to 120 degrees. However, like the tuning for cells selective for views of the head (Perrett et al., 1991), there seemed to be two distinct populations ("narrow" and "broad" tuned). Using a cut off point of 90 degrees, the

range of tuning for the "narrow" tuned cells was 45 to 75 degrees. This was found to be similar to the head view cell range.

Preferential tuning of direction along cartesian axes has been found to exist in other areas of the brain. The accessory optic system (AOS) which exists in all vertebrates and in most mammalian species (Fite, 1985) has units with large visual receptive fields which are driven best by the movement of large textured patterns at relatively slow speed (Simpson, 1984; Soodak & Simpson, 1988; Frost et al., 1990). AOS is involved in routing the visual signals to the vestibular systems through several pathways. Studies with rabbits, for example, have shown that when the animals have been subjected to whole field optical rotation along selected axes, there are essentially three axes to encode this whole field rotation. The direction of these axes coincide with the best-response axes of the semicircular canals showing thus that the visual motion detection system at this level shares the same set of co-ordinate axes (Simpson et al., 1988). A similar picture holds for the cat AOS so that the distributions coincide with retinal motion following rotation about vestibular canal planes or horizontal movements of the head (Grasse & Cynader, 1982, 1984). The response properties of primate AOS neurons seem to differ of those observed in rabbit, cat and birds in that the responses are also evoked by small single objects (Westheimer & Blair, 1974, Hoffmann & Distler, 1989). Hoffman and Distler (1989) have suggested that this is due to the strong projections from cortical area MT specialized in motion analysis to the AOS. The primate AOS neurons show broad tuning (mean half height, half width of 63.5 degrees), with large receptive fields. The responses were independent of stimulus size and the population covered a large range of effective speeds, with the highest effective speeds being far above those for cat and rabbit (Hoffman & Distler, 1989).

Psychophysical studies with human subjects have revealed interesting parallels with the neurophysiological studies with primates. Using moving random dot

displays, Levinson and Sekuler (1980) measured the elevation in luminance detection threshold for various directions of movement following adaptation to motion of the display in one direction. The elevation in threshold varied with the direction of drift of the test stimuli from the adaptation direction. It was found that maximal elevation occurred when the test stimuli moved in the same direction as the adaptation stimulus, and fell to a minimum for opposite directions of motion. The half height half width measure varied between 40 and 60 degrees, which is within the range of half height - half width measures for STP unidirectional cells reported here as well as for AOS and MT cells reported in other primate studies (Hoffman & Distler, 1989; Albright, 1984).

Form and motion processing in STP. Studies of the STP cell responses to form (static head views) and motion stimuli have revealed that the discrimination, the breadth of tuning and distribution of preferred head views/directions are comparable between these two populations of cells in the same area (Perrett et al., 1991; Oram et al., 1992). However, temporal characteristics of STP cell responses to form and motion stimuli have revealed differences in the response latencies to these two classes of stimuli (Oram & Perrett, 1992; Oram et al., 1992). Comparison of average response latencies have indicated that the directionally selective motion sensitive cells respond at earlier latencies (mean latency = 91 ms) than cells selective for different (static) views of the head (mean latency = 119 ms). This suggests that motion sensitivity of cells in the anterior portions of STP is established by a different route not involving the ventral pathway via inferotemporal cortex and provides, therefore, further evidence for the *convergence* of form and motion pathways in area STP.

CHAPTER 7

STP CELL RESPONSES TO THE SIGHT OF ONE'S OWN LIMB MOVEMENTS

7.1. INTRODUCTION

Active behaviour in the natural surroundings causes continuous stimulation of sensory systems as an inevitable consequence of mere action. An animal is stimulated not only from sources in the environment but also by itself. In fact, an animal's own behaviour can give rise to sensory stimulation that is very similar to stimulation of completely external origin. In some cases this self-induced stimulation is used to provide information about an animal's own activity in relation to its environment and hence to monitor the ongoing motor activity, but there are instances where self-induced stimulation has little informative value to the animal and may even interfere with the processing of externally-induced stimulation.

Examples of sensory systems where stimulation resulting from an animal's own actions is discriminated from equivalent externally-induced stimulation can be found in a diversity of species in the animal kingdom. The most familiar and most studied example is the perception of a stable visual world during voluntary eye movements. Even though the retinal image moves across the retina, we do not experience movement of the visual environment. This phenomenon is a necessary prerequisite for the stabilization of the visuo-spatial environment. The nervous system must, therefore, process visual information resulting from self-induced eye movements differently from that arising when the eyes are still and the environment moves. Descriptions of the phenomenon and theories of the underlying neural basis have a long history extending back to Mach, James, von Helmholtz and Descartes (for

a historical review see, Grüsser, 1986). In modern theories the core idea has been that in addition to sending messages to oculomotor centres for moving the eyes, the motor command centres send a corollary discharge (Sperry) or an efference copy (von Holst and Mittelstaedt) to the visual centres to compensate for or cancel the retinal displacement resulting from the eye-movement (Sperry, 1950; von Holst and Mittelstaedt, 1950). Computationally a less demanding role for corollary discharges has been suggested by MacKay (1973). He proposed that perceivers build up an internal representation of their environment with the expectation that it is unchanging. The function of corollary discharges is to provide information to the central mechanisms when the incoming afferent sensory signals do not require an adjustment to be made to the internal representation of environment (i.e. in the case of self-induced stimulation).

Since the early theories neurophysiological investigations have found single cell activity related, not to the movement across the receptive field on the retina per se, but to the "real movement" of objects in the visual field, independently of the eye movements. Image motion caused by an animal's own eye movements has been observed to elicit reduced neuronal responses compared to real-motion in the superior colliculus (Robinson & Wurtz, 1976; Richmond & Wurtz, 1980; Straschill & Hoffmann, 1970) and several cortical visual areas, V1, V2, V3a and MSTd (Fischer et al., 1981; Toyama et al., 1984; Galletti et al., 1984, 1988, 1990; Erickson & Thier, 1991) of monkeys and cats.

The examples of cases where self-produced stimulation is treated differently from the equivalent external stimulation are by no means restricted to the visual system or mammals. Differential responses to 'self-vocalised' versus 'playback' vocalizations have been recorded within the auditory system of bats and monkeys. It has been found that the responses of neurons in the nucleus of the lateral lemniscus of bats differentiate between self-emitted sounds and the same sounds played back from

an audio tape, even when the auditory nerve response is the same for both sound stimuli (Suga & Schlegel, 1972; Suga & Shimozawa, 1974). A similar response differentiation between self-produced vocalizations and externally produced "playback vocalizations" has been found in neuron responses in monkey's thalamus and auditory cortex (Müller-Preuss, 1983, 1986).

Fish and frogs have a unique sensory system - lateral line sense organ - specialized for detecting fluid motion in their aquatic environment. The activation of this organ by an animal's own movements, however, may interfere with the extraction of relevant signal features from the environment. Efferent motor signals evoked by voluntary movements have been found to inhibit signals in afferent fibres from the lateral line sense organ (Russell, 1968, 1971). Visual stimulation causing optokinetic turning motions in goldfish has been suggested to evoke motor corollary discharges sent to the semicircular canals in order to keep the vestibular organ capable of responding to additional stimuli (passive body movements, disturbances of equilibrium) during active body movements (Klinke, 1970). Electric fish with electrosensory systems for communication and location have been studied in the same context. Again, processing systems afferent to the electroreceptors have been shown to be affected by "corollary discharge signals" associated with the motor command that drives the electric organ responsible for the emission of an electric signal (Meyer & Bell, 1983; Bell, 1989). With this feed-forward processing the electrosensory system remains able to detect signals arising from other fish but does not respond to self produced signals.

The biological purpose of this discriminative capacity seems to be common amongst these diverse examples: to ensure maximally effective extraction and processing of behaviourally relevant stimulation from the environment and to be able to ignore self-produced reafferent stimulation.

Recent studies have shown that cells at a high level of the somatosensory system of macaque monkeys (in the superior temporal sulcus, STS) do not respond to tactile stimulation arising from the monkey's active exploration of familiar surfaces, but do respond to passive stimulation, for example from the touch of the experimenter (Mistlin & Perrett, 1990). Furthermore, the response of these cells has been shown to be dependent on "expectation" of the stimulus and hence the cells have been suggested to be a part of a general system for detecting (unexpected) stimulation arising from other animals. These findings prompted us to study, whether similar response selectivity is present within the visual modality as well.

Cells in the anterior portions of the superior temporal sulcus are well known for their extremely selective visual responses, for example to hands, human and monkey faces, and body movements (Gross et al., 1972; Desimone et al., 1984; Perrett et al., 1982, 1984, 1985a,b, 1991; Baylis et al., 1985; Hasselmo et al., 1989; Hietanen et al., 1992). Surprisingly, this area also contains cells which appear to lack any kind of selectivity for visual form. These cells are often, however, sensitive to simple motion (including translation in the fronto-parallel plane or in depth) over very large receptive fields which often cover the whole visual field (Bruce et al., 1981; Perrett et al., 1985b). It was decided to study whether this particular group of cells might discriminate between self-induced and externally-induced motion stimulation.

The chapter describes a novel situation showing that one population of neurons in the visual system discriminate between self- and non-self-produced image movement. In the present experimental situation the animal's actions, however, do not result in the movement of the entire sense organ and hence in the movement of the whole visual field as is the case with eye or whole body movements (Robinson & Wurtz, 1976; Richmond & Wurtz, 1980; Straschill & Hoffmann, 1970; Fischer et al., 1981; Galletti et al., 1984, 1988, 1990; Erickson & Thier, 1991; Roy & Wurtz, 1990). Instead, the functional connection between the motor commands and consequent

sensory events is much more complex as the discriminated self-produced motion is restricted to a limited part of the visual field.

7.2. METHODS

Testing procedure. Before beginning recordings the subjects were trained to sit in a primate chair with head restraint and perform in a LED colour discrimination task (see chapter 5 for general methods).

After isolating a cell its responsivity to visual stimuli was initially tested using a shutter placed 15 cm in front of the monkey's eyes. On each trial 3D stimuli were presented from behind the shutter which became transparent for 1.0 s, after a 0.5 s signal tone. It otherwise remained opaque white. First it was established whether the cell response showed any selectivity for stimulus movement over responses to static stimuli. In this purpose, the cell was tested for responses to the sight of hand-held objects in peri-personal space (0.2-1.0 m) moving in different directions (left/right, up/down, away/towards) and the experimenter walking in different directions at a range of distances from the monkey (1.0-3.5 m). If stimulus motion was observed to affect the responses, selectivity for the direction of movement was tested systematically. Second, the cell responses were tested for form selectivity. Various 3D laboratory objects of different shape, size, colour and texture (human faces and bodies, fruit, tools, boxes, fur etc.) were presented to the monkey through the shutter. Each stimulus was moved in the cell's preferred and at least in one other (usually 180 degrees from the preferred) direction.

Cells were selected for further testing on the basis of whether or not they fulfilled two criteria, a) the cell should respond when a stimulus entered the visual field from below, at a distance of 10 - 20 cm from the monkey, and b) the cell should

not show selectivity for stimulus form, colour or velocity. Further testing included comparing the cell responsiveness to the sight of the monkey's own arm with that to various control objects entering the view from below.

While sitting in the primate chair the monkeys were by nature interested in exploring the surroundings with their hands, and whenever a slit in the front panel of the primate chair was opened, the monkeys usually pushed their arm through it. They would spontaneously raise the hand into view, inspect the hand and occasionally manipulate the lick-tubes just in front of their mouth, or, if given a piece of food, feed themselves. The monkeys did not need much encouragement to get them to move their own hands into view. Because of the head restraint and the edges of the primate chair walls, it was possible to determine quite accurately the borders of the monkey's field of view when looking out from the primate chair into the testing laboratory. This visual space was restricted because of the occlusion by the primate chair walls and was thus independent of the eye movements. Objects located behind these walls were impossible for the monkey to see, but as soon as a moving object crossed the border of this visual field, it became visible to the monkey.

By making use of the monkeys' spontaneous hand movements made in feeding and exploring objects, a relatively simple but natural experimental paradigm was designed. Single cell responses to the sight of the monkey's own arm entering its visual field were compared to the sight of a variety of control objects coming into view. Quantitative measurements of the cell responses to such visual stimulation were made using two different methods in the course of the experiments. First, neuronal responses were assessed by counting the number of spikes during a 0.5 or 1.0 s period after the stimulation onset. This was done by the experimenter manually triggering cell activity measurement (see below) at the moment when the object or the monkey's own hand entered the monkey's view.

Second, a device was constructed for minimising the small inaccuracies in stimulation onset timing which were inevitable with the manual triggering. The device detected the moment of stimulation onset with an array of light-detectors. This device was fitted to the slit in the front panel of the primate chair (see Fig. 7.1). The device consisted of a closable door (to prevent the monkey from putting its arm out from the chair) and an array of infra-red light-emitting diodes on one side of the slit opening each paired with a light detector on the other side of the slit. The light diodes and detectors were mounted on an adjustable frame above the door hole. By adjusting the tilt of the frame the array of infra-red light beams were lined up with the monkey's line of sight dividing the space into that visible and that occluded from the monkey's sight. Breaking any one of the infra-red light beams activated the computer and started data collection. This apparatus was thus able to detect whenever the monkey's arm came into view or whenever the experimenter introduced control objects into view from below. With both methods it was easy for the experimenter to mimic the presentation (i.e. velocity and direction) of the control objects in the way that the monkey introduced its own arm in view.

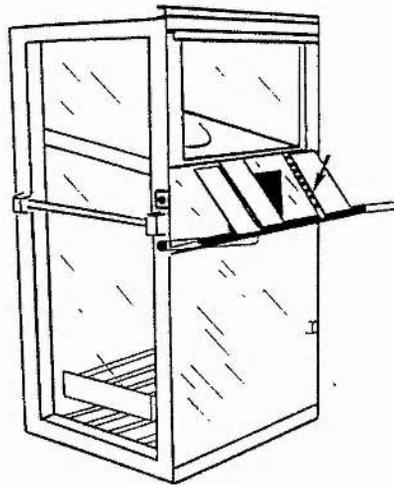


Figure 7.1. A drawing of a modified primate chair. Arrow points to an array of infra-red light detectors used to detect when the stimuli entered the monkey's visual field. The monkey could introduce its own hand into the field of view through an aperture in the front panel of the chair (dark area in the figure).

The optical triggering device was also used with the colour discrimination task. The monkey was encouraged to introduce its hand into view to initiate LED colour discrimination trials in a self paced manner. In this setting the sequence of events was as follows. The stimulus presentation (monkey's own hand or control object introduced by the experimenter) activated the onset of a) a short (100ms) tone signal, b) the lower or central LED light for 1.0 s and c) data collection of cell activity and eye movements for 1.0 s time period. The purpose of the tone signal was to inform the monkey of the LED light onset in order to get the monkey fixating the LED with a minimum latency independent of the mode of trial initiation (external or self).

Different test stimuli were interleaved in counterbalanced order. At the testing distance of 10-20 cm the width the monkey's own hand covered was approximately from 17 to 9 degrees of visual angle. In most experiments the control stimulus used for the actual data collection was a relatively realistic life-size artificial monkey hand and arm. Care was taken not to introduce the control object above the monkey's eye level so that the LED light remained visible to the monkey throughout the stimulus movement. The success of this precaution was supported by the monkey's accurate performance in the colour discrimination task independent of the other visual stimulation.

Recording procedures and data analysis. Extracellular single unit activity was recorded from two female (F and J) and three male (B, D, and H) rhesus monkeys (*Macaca mulatta*, wt 4-8 Kg) using standard chronic recording techniques as described in Chapter 5.

Horizontal and vertical eye movements were monitored (and recorded during the electrophysiological experiments) by using an infra-red corneal reflection system adapted to allow recording of both signals from one eye. The eye position signals

were digitized every 5 ms and stored together with the single unit activity. As monitoring the monkey's eye movements during different stimulus type presentations (see below) was an essential control precaution for the experiments, care was paid to the accuracy and reliability of the eye movement recordings. At the beginning of each recording session the eye-movement recording system was calibrated by requiring the monkey to perform the red/green colour discrimination task with each of the LED locations.

Figure 7.2 presents monkey's eye movements from 12 calibration trials for each five fixation point locations. In this calibration procedure the fixation point location was varied in a pseudorandom order. During subsequent neurophysiological experiments the LED position was constant across a block of trials. It can be seen that the monkey performed the task and fixated the LEDs with a latency of around 400 ms after the fixation light onset. [The monkey's performance was 92% correct responses during the calibration trials]. There is some variation in the eye positions during fixation periods across different trials. This is probably due to the fact that the luminance level of the LEDs was sufficiently high for the monkey to discriminate its

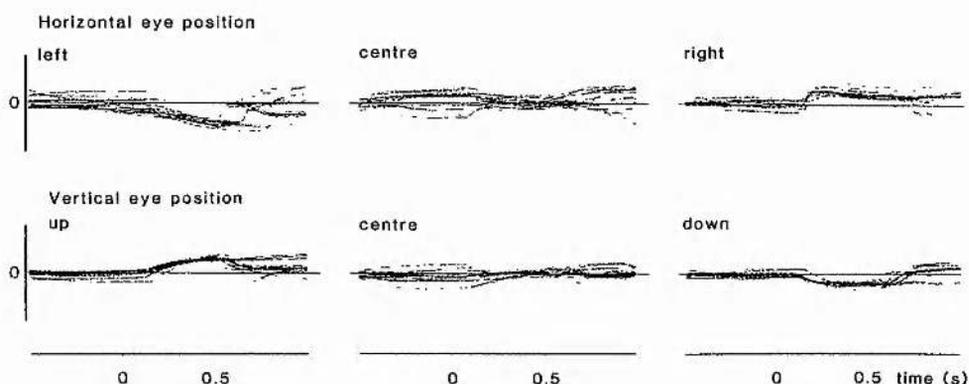


Figure 7.2. An example of the recordings of monkey's eye movements during the fixation task. The upper 3 traces illustrate the horizontal eye position during fixation of the left, centre and right LED locations and the lower traces illustrate the vertical eye position during fixation of the up, centre and down LEDs. Eye movement traces are pictured from 12 trials for each of the five fixation point locations. On the horizontal axis left and right fixation points were located 15 degrees of visual angle away from the centre fixation point. On the vertical axis the distance for the up and down fixation points was 10 degrees of visual angle from the centre fixation point. The ordinate axis in the eye position recordings give a scale for ± 20 degrees. Time scale is shown at the bottom.

colour without accurate foveation. This simple calibration procedure achieved an accuracy of ± 2 degrees (over the central field of view, that is over ± 15 degrees) from these trials which was adequate for the purposes of this study (see below).

In some experiments the filtered cell activity, together with the eye movement signal and stimulus onset signal, were additionally recorded on a four-channel FM tape recorder (RACAL) for off-line analysis. This method also provided the most convenient way for inspecting of pre-stimulus cell activity for self-initiated trials. In some experiments a close-up of the upper part of the primate chair from a side view was filmed with a video camera and recorded on a 3/4 inch U-matic videotape. Afterwards the film was played back frame by frame, and the number of frames (25 frames/s) taken for the monkey's hand or control object to move a measured distance was recorded. Given the distance from the monkey's eyes to the stimuli it was possible to calculate a reasonably accurate estimation of the retinal velocity for the movements of the hand-held control objects and monkey's own arm.

Quantitative measurements of cell responses to different types of visual stimuli and spontaneous activity were analysed by using 1-way ANOVA and post-hoc tests (protected least significant difference, PLSD, Snedecor and Cochran 1980).

After each recording track, frontal and lateral X-radiographs were taken to allow the position of the metal microelectrode to be reconstructed from subsequent histology. The histological procedures were as described in Chapter 5.

7.3. RESULTS

7.3.1. General response properties

47 neurons were isolated from the anterior superior temporal sulcus which satisfactorily fulfilled the requirements of a) lacking form selectivity and b) responding to the entry of objects into the visual field from below. These were tested for possible differences in responses to self-produced and externally-produced moving visual stimuli.

18 of these cells were selective for stimulus motion in view and 8 cells were selective for entry into view. In the latter case there was no response to the continuous movement in view, but only a transient burst of activity to the stimulus entry into view. The remaining 21 cells responded weakly to static stimuli with stimulus motion further increasing the activity. Typically the cells responded over a wide range of stimulus velocities (20-400 degrees/s). Transient responses were more typical than sustained responses. When stimuli were presented from behind a liquid crystal shutter the cell responses were observed to occur with latencies of 90 - 150 ms. Response habituation for the effective stimulus presentation was not observed and the responses maintained their strength for at least 10 consecutive identical stimulus presentations.

Figure 7.3 shows an example of a STS cell sensitive to visual stimulus motion. The cell gave a transient response to stimulus motion with a slight directional selectivity for movement up, whereas a static control object did not increase the cell activity above spontaneous level.

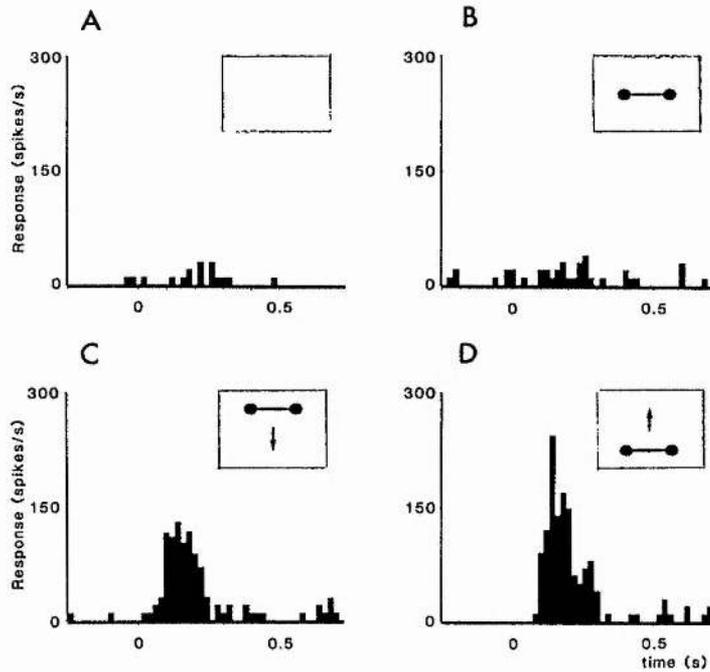


Figure 7.3. Peristimulus-time histograms of responses of a STS cell sensitive to stimulus motion. The responses were collected by presenting the stimuli behind a shutter for 1 second. Sight of a static control object (**B**) did not increase the cell activity above spontaneous level (**A**), whereas the cell gave a strong response to the sight of the same control object moving upwards. The cell exhibited an additional slight selectivity for direction. Control object moving upwards (**D**) elicited a stronger response than the sight of the same control object moving downwards (**C**) (PLSD, $p < 0.02$, 1-way ANOVA, $F_{3,16} = 15.4$, $p < .0005$). The histograms show data collected from five trials. Bin width = 20 ms in each histogram.

7.3.2. Response selectivity for motion direction

Thorough tests for the directional selectivity of the neurons examined here were not performed systematically across the cell population. Of the 26 cells tested for directionality 14 cells were observed to be responsive to all directions of motion in the fronto-parallel plane. 9 cells exhibited a preference for certain directions with three cells responding to only upward movements. Cells with preferences of other directions of movement were common in the STP but were not included to the present experiments. This directional selectivity limited the number of neurons to be studied, because the testing paradigm necessitated responses to upward movements.

7.3.3. Feature selectivity

As explained in the methods, particular attention was paid to the possibility that the observed differences in cell responses might have been caused by visual selectivity for form or simple features. 43 of the cells fulfilled the criterion of lacking form selectivity completely. These 43 cells were found to exhibit indistinguishable responses to a variety of laboratory objects as long as the object movement occurred in the cell's preferred direction. A further 4 cells were discovered to exhibit some degree of feature selectivity. Two of these showed a selectivity for stimulus size at the testing distance preferring large objects (e.g. a book) over smaller ones (e.g. a pen), but as the control objects presented to the monkey were matched in size to the monkey's arm, there was no reason to exclude these two cells from the data analysis. Two other cells showed a selectivity for form in that they responded equally well to many objects of differing visual characteristics, but not at all to faces. These two cells were also included in the data analysis again because the form selectivity present in the cells could not account for any response difference between the sight of the monkey's hand and control objects used for testing.

7.3.4. Differential responses to the sight of object motion and motion of own hand

39 (83%) of the tested 47 cells exhibited differences between responses to the sight of a control object moving and to the sight of the monkey's own arm moving into view in the same direction. 38 of these 39 cells failed completely to respond to the self-induced motion stimulation (i.e. cell responses were not significantly different from spontaneous activity). One cell also responded to the sight of the monkey's own hand, but still gave significantly stronger responses to externally-moved objects. No cells were found responding selectively to the sight of own arm movements, although it is possible that such cells were not seen because they did not respond at all to object-motion. The remaining 17% of the tested cells gave equally strong responses to both stimulus types.

Figure 7.4 shows histogram presentation of responses (spikes/s) of one cell (H40_27.82) to the sight of a control object and the monkey's own hand moving in the same direction (upwards) and the cell's spontaneous activity. Quantitative measurements of the responsivity of this cell was collected by using both the manually triggered spike counting method and the light-detector device. Results collected with both methods showed the same pattern with a significantly larger response to the sight of a control object moving than to the sight of monkey's own arm moving or spontaneous activity. A 2-way ANOVA performed on the data (with stimulation type and method of data collection as main factors) showed a significant effect of stimulation type ($F_{1,23} = 40.2, p < .0005$), but no effect of method ($F_{1,23} = 0.37, p = 0.551$), and no interaction between stimulation type and method of data collection ($F_{1,23} = 1.0, p = 0.328$). Thus testing the same cell with these two methods proved that the manually triggered spike counting method was accurate enough for catching the stimulation onset and neuronal response.

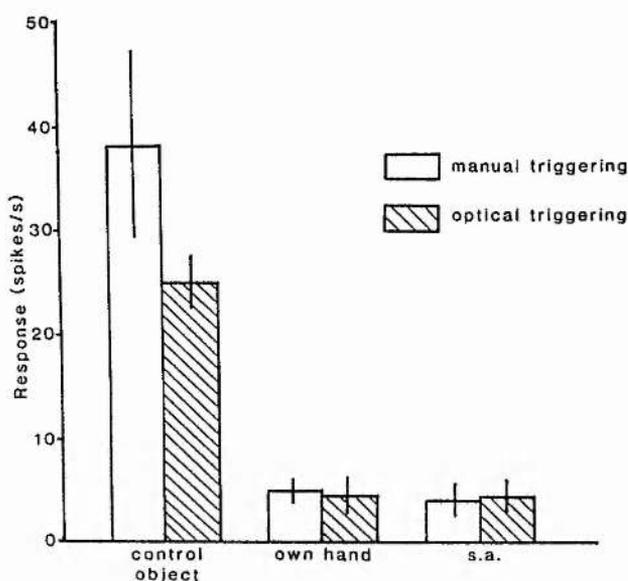


Figure 7.4. Histogram presentation of mean responses (spikes/s \pm 1 standard error) of one cell to the sight of a control object and monkey's own hand moving upwards and the cell's spontaneous activity. The spike counting was triggered both manually and with a light-detector device. Results collected with both methods showed the same pattern with significantly larger responses to the sight of a control object moving than to the sight of monkey's own arm moving or spontaneous activity ($p < .0005$, each comparison). (1-way ANOVA (manual triggering), $F_{2,18} = 12.8, p < .003$, number of trials per condition ($n = 7$); 1-way ANOVA (light-detector), $F_{2,16} = 31.6, p < .0005, (n = 7, 7, 5)$).

7.3.5. Responsivity to external stimuli during self-induced stimulation

It was essential to study whether the cells continued exhibiting visual responses to external stimuli while the monkey's own hand was in view. The reasons for this investigation were two-fold. First, it was possible that the mechanisms producing a lack of responsiveness to self-produced visual stimulation caused some kind of general cessation of processing all visual information by the recorded cell. Second, the lack of responsiveness to the sight of a monkey's own arm might have been caused simply by an unstable recording during the monkey's movements. Therefore, the monkey was encouraged to lift its arm in view and at the same time the experimenter introduced stimuli into the monkey's visual field as described. All the 7 neurons tested this way continued responding to external visual stimulation while monkey's own arm was moving and visible. Further, in all 7 cases the cells exhibited no decrement in their responsiveness as compared to the condition where only control objects presented by the experimenter were visible.

Figure 7.5 presents results of one such experiment. The cell (D201_30.02) responded briskly to the sight of experimenter's hand or control objects moving in the view in all directions. The presence or absence of monkey's own hand in sight at the same time did not make any difference to the responses to experimenter's hand moving in view. In both conditions the sight of experimenter's hand elicited significantly stronger responses than monkey's own hand moving in view or the cell's spontaneous activity

7.3.6. Unexpected self-produced stimulation

In these experiments the two lines of study described before were combined. Again, an object was introduced to the monkey's field of vision, but this time the object motion was caused by the monkey itself. An object, e.g. a small piece of food, was put into the monkey's hand out of sight, and then the monkey was allowed to bring

the object in its hand into view. On each trial a new object was placed into the monkey's hand. Seven cells were studied with this procedure all of which had proved

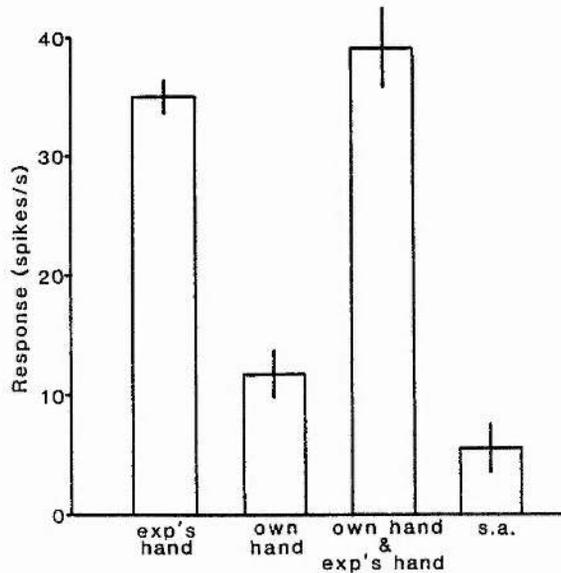


Figure 7.5. Mean response (± 1 SE) of an STP cell to different visual stimuli. Experimenter's hand (and various control objects) entering the monkey's visual field from below elicited a response above the cell's spontaneous activity (s.a.), whereas the sight of the monkey's own arm entering into view in the same direction did not activate the cell. The presence of the monkey's own arm in view, however, did not affect the visual responses to the entry of control objects. In any case the sight of control object elicited significantly stronger responses than monkey's own hand moving in view or the cell's spontaneous activity ($p < .0005$, each comparison). (1-way ANOVA, $F_{3,19} = 51.4$, $p < .0005$, number of trials per condition (n) = 10, 8, 5, 7).

to be unresponsive to the sight of the monkey's hand alone in preliminary testing. Five of these cells did give responses when the monkey brought an object into view in its hand. Figure 7.6 shows results for one cell tested in this way. The cell (H5_26.18) responded to control objects (fur, glove, feather, black bar etc.) and the experimenter's hand alone entering into view, but gave no response to the monkey's own hand entering the visual field. The cell, however, responded to the monkey's hand bringing an object into view more strongly than to the monkey's arm moving alone or spontaneous activity.

7.3.7. Eye movements during self-produced and external visual stimulation

Monitoring of eye movements was essential to ensure that differences in cell responses to the sight of stimuli moved by the experimenter or by the monkey were not caused by differences in fixation or tracking. For example the monkey's eyes might follow movements caused by the experimenter but not the movements of its own hand.

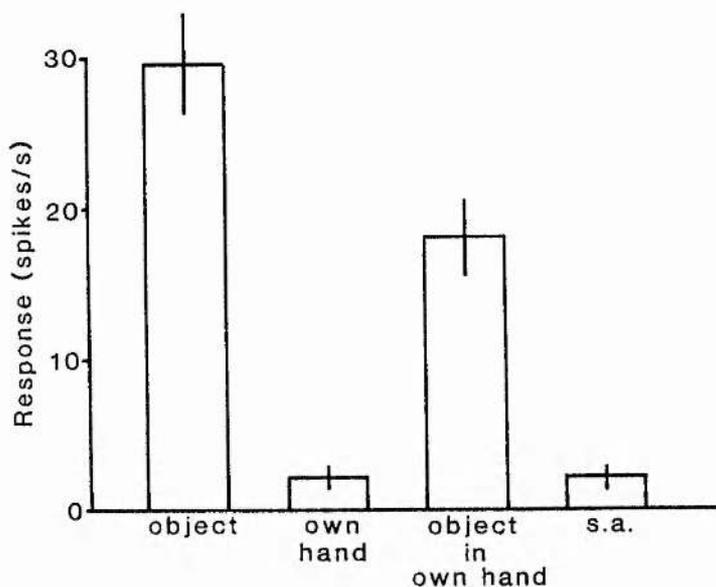


Figure 7.6. An STP cell responded to various objects (fur, glove, feather, black bar, model monkey arm, and the experimenter's hand) entering into view, but gave no response to monkey's own hand entering the visual field. The cell gave a response when the monkey brought objects (e.g. a piece of apple) into view with its own hand. These responses were stronger than responses to the sight of monkey's arm moving alone or s.a. ($p < .0005$, each comparison), but weaker than responses to objects moved by the experimenter ($p < .004$). The monkey did not know the visual appearance of the objects which were placed in monkey's hand out of sight, and changed after each presentation. (1-way ANOVA, $F_{3,26} = 32.0$, $p < .001$, $n = 10, 8, 5, 7$).

Figure 7.7 presents vertical eye movements and spike activity of a cell to externally and self-induced visual stimulation. The testing was performed by using the light-detector device, and the cell was tested with the upward movement of the control artificial monkey arm or the monkey's own arm. During this particular testing the LED fixation light which usually located at the level of monkey's sight (see methods) was switched to a bottom position (10 degrees below central position). In

this way the monkey was biased to direct its gaze in the direction from which the stimulus would appear.

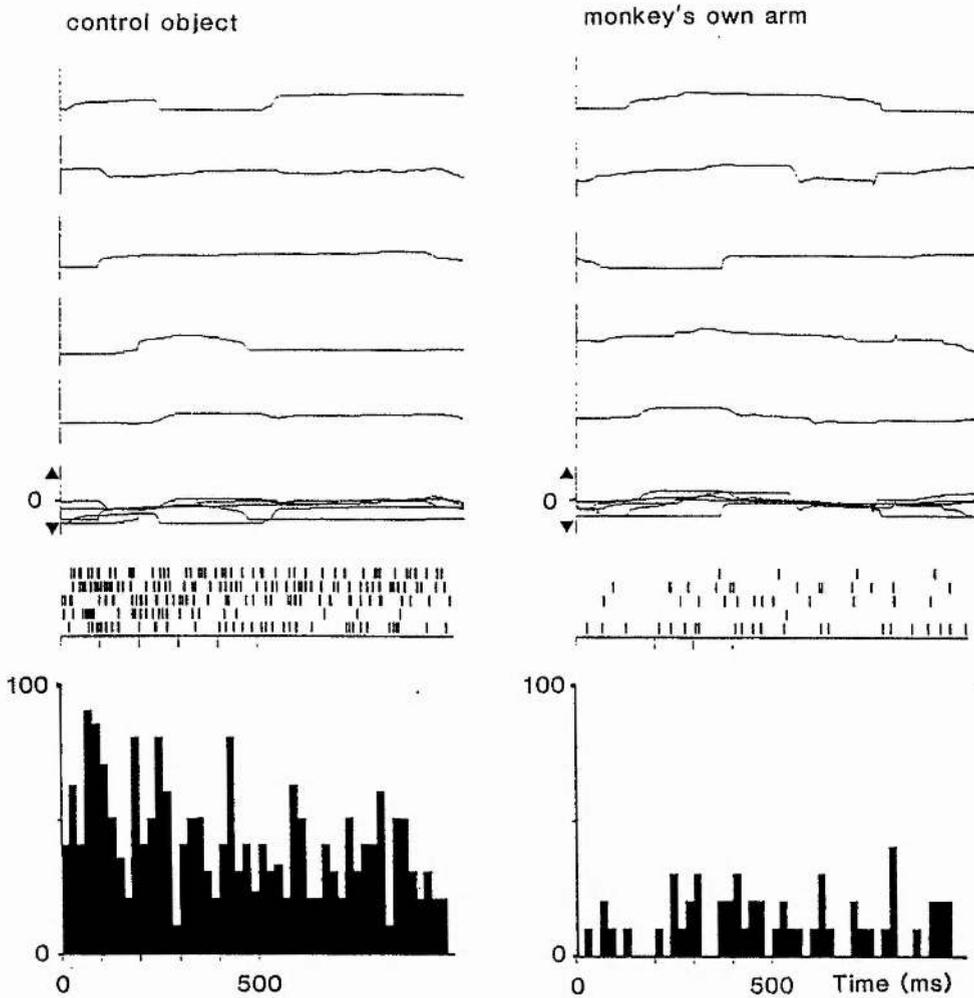


Figure 7.7. Vertical eye position tracks and activity of an STP cell which responded to the sight of an object entering into the monkey's visual field (left column), but not to the sight of the monkey bringing its own arm into view (right column). The vertical eye position is illustrated for five (randomly interleaved) trials in both conditions, and the sixth row shows the summed eye movements during these trials. The post-stimulus time rasterograms show spike activity (short vertical dashes) during these five trials retaining the same order. At the bottom the cell activity is depicted in post-stimulus time histograms. The ordinate axis in the eye position recordings give a scale for ± 20 degrees and the ordinate axis of the PSTHs show cell responsiveness in spikes/s.

Figure 7.7 illustrates that the monkey made a variety of different fixations and saccades during the presentation of the control stimulus by the experimenter. Despite this range of eye movements the cell responded on every trial. When the monkey initiated the trial by bringing its own arm into view, eye movements again showed the

same variation in pattern of fixation, saccades and tracking, yet in this condition the cell always remained unresponsive. It is also evident from the recording that the cell's response was not modulated in any obvious way by the presence of saccades. It might be anticipated that the monkey would be more interested in the movement of control stimuli than its own hand but the eye movement records indicate a comparable interest (or disinterest) in both stimuli.

Thus eye movements did not cause the difference in the responses to self-induced movement and object motion. Cell response or lack of response was dependent on the stimulus type and independent of relatively large variations in the eye movement patterns.

7.3.8. Location of cells

Histological reconstruction in monkeys B, F, D and J indicated that 40 of the 45 tested cells in these monkeys were located in the cortex of the dorsal bank of the superior temporal sulcus (areas TPO and PGa of Seltzer & Pandya, 1978). X-ray measurements of recording positions in the remaining monkey (2 in subject H) indicated that the tested cells from this subject were also located within the same area. Thus from the histological evidence and reconstructions based on X-ray measurements a total of 42 cells (out of the 47 tested) were recorded from areas TPO and PGa. Of these 37 (88%) exhibited selective responses for externally induced motion. The cells described here were within the same area as those responsive to the static views of the head that have been described in earlier studies (Perrett et al., 1982, 1984, 1991).

Even though the recordings were aimed at the dorsal bank of the STS, histological reconstruction indicated that five of the studied cells were in the ventral bank of the STS. In monkeys F and J three of these cells showed selective responses

to the externally-induced motion, but in monkey D both cells responded equally well to the sight of the monkey's own hand and moving control objects. Figure 7.8 shows the results of the histological reconstruction in monkey (D) from which the majority of the cells were recorded (27/47).

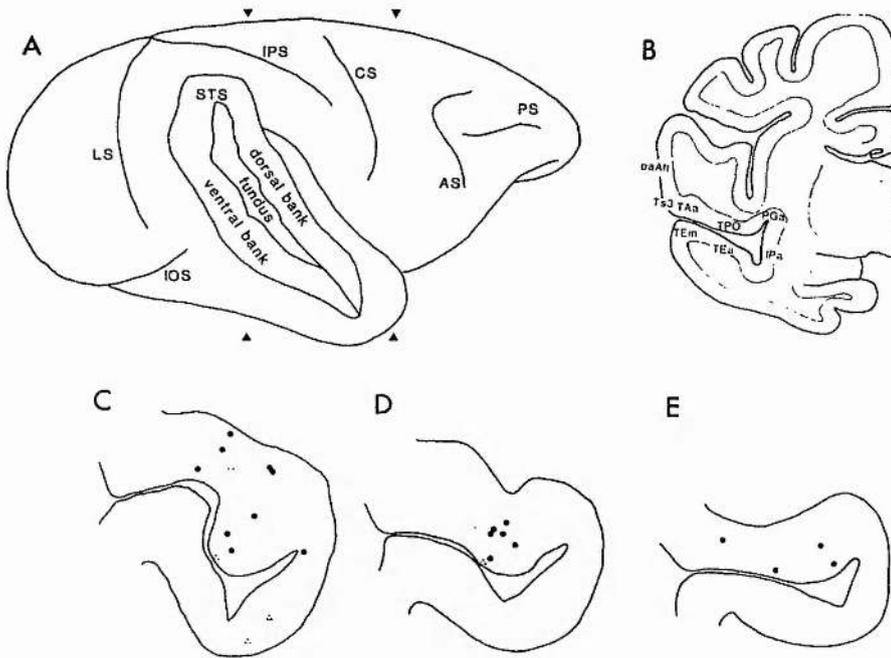


Figure 7.8. **A)** A lateral view of the right hemisphere of a rhesus macaque brain showing major sulci. Abbreviations: STS = superior temporal sulcus, IOS = inferior occipital sulcus, CS = central sulcus, IPS = intra parietal sulcus, LS = lunate sulcus, AS = arcuate sulcus, PS = principal sulcus. The superior temporal sulcus (STS) is opened to reveal the bottom and both banks of the sulcus. The two pairs of arrows show the interaural plane and a plane 20 mm anterior to it. **B)** A coronal section of the right hemisphere showing the subareas within the STS according to Seltzer & Pandya, 1978. **C-E)** Three enlarged coronal sections of the STS taken at the levels of +12 mm, +15 mm and +18 mm. The position of the recorded cells located between +10 mm and +20 mm along the rostro-caudal extent of the STS. For the illustration, the studied cells from both hemispheres which were located between 10-14, 14-17, and 17-20 are shown in figures **C**, **D** and **E**, respectively. The filled circles mark the location of cells responding selectively to externally-induced movement, and the open triangles show the location of cells failing to show this discrimination.

7.4. DISCUSSION

Neurophysiological studies of single cell responses in the anterior parts of the dorsal superior temporal sulcus have almost exclusively concentrated on selective responses to complex visual stimuli. The most frequently studied cell type has been those responsive to the face and other views of the head (Bruce et al., 1981; Perrett et al., 1982, 1984, 1985a, 1991; Desimone et al., 1984; Rolls & Baylis, 1986; Hasselmo et al., 1989; Hietanen et al., 1992). Cells with highly selective responses to specific body movements (e.g. walking in one direction with one body view) have also been studied extensively (Perrett et al., 1985b, 1989c, 1990a,b). Yet the earliest of single cell studies within this area in anaesthetized monkeys reported the existence of visually responsive cells sensitive to stimulus motion but lacking any selectivity for form (Desimone & Gross, 1979; Bruce et al., 1981).

The existence of cells lacking form selectivity within anterior STS seems rather surprising because of two reasons. First, from the point of view of object recognition it is very difficult to think what the functional value of units which respond to all moving objects would be. Second, from the point of view of motion processing it is difficult to think of a functional role of motion sensitive cells lacking directional tuning or pronounced velocity sensitivity at a stage of analysis *after* very detailed processing of motion information has been performed earlier in the "motion pathway" within posterior parts of the same sulcus (i.e. areas MT and MST).

It appears, however, that when studied with awake, behaving monkeys, STS neurons non-selective for form but sensitive to movement have very complex selectivity discriminating between externally-induced stimulus motion and visual movement which results from animal's own action. A very high percentage of the studied cells in the anterior dorsal STS (88%) responded to the sight of any object

moved into view by the experimenter, but failed to respond above spontaneous activity to the sight of monkey's own hand and arm movements.

It could be argued that the differences in responsivity to these two classes of stimuli reflects the effects of arousal rather than discriminative sensory processing between externally-induced and self-induced stimulation. This possibility, however, seems very unlikely. First, this kind of explanation has been considered for STS cells responsive to faces and no evidence for relation to arousal has been found (Perrett et al., 1982, 1984). Second, if the responses to a moving control object were only due to its arousing nature, one would expect a sight of a static face or food to evoke a comparable "arousal response". This was not the case as cells studied here did not respond to such static stimuli. Third, the neuronal responses were time-locked to the visual stimulation, occurred at short latencies and were transient in most cases. These response characteristics are unlikely if the cells merely reflected arousal.

The observed response discrimination might reflect differences in interest or the attention paid to the externally-moved control objects and monkey's own hand. Eye movements can be used as an indicator of interest in the moving stimuli. Records of the monkey's eye movements indicated that the monkey's fixation of its own hand and control objects was equivalently variable. Recordings therefore do not indicate one stimulus class as more interesting. Eye position recording also showed that the responses were not related to the eye movements (Fig. 7.7). The observed lack of habituation in responses to control objects moving into the field of view also speaks against the responses being related to the level of interest.

In order to get insight into the functions of the STS cells studied here the results are discussed in the context of neurophysiological studies of cells in other brain areas which resemble the present experiments.

Visual guidance of hand actions. The posterior parietal cortex has been shown to be heavily involved in combining visuo-spatial and motor information and in visual guidance of hand projections (Hyvärinen & Poranen, 1974; Mountcastle et al., 1975). In a recent study Taira et al. (1990) found that a majority (69%) of their "hand-movement related" neurons showed activity changes in response to hand manipulation, with the activity of the cells being greater when the hand movement took place in the light. This was taken as an evidence that these cells received a motor input as well as a visual input related to the object and/or the moving hand. Furthermore, a role in monitoring (rather than in commanding, cf. Mountcastle et al., 1975) the ongoing motor activity was assigned to the parietal neurons by Taira et al. (1990).

In contrast, the present study showed that the cells in the anterior dorsal bank of the STS selectively failed to respond to the sight of the monkey's own arm movements. This was also the case when the monkey projected its arm and hand into view in order to reach for a piece of food, i.e. during goal-directed movements under visual guidance. It is noteworthy that cells selective for the sight of manipulative hand actions found from the ventral bank of the STS (area TEa) do respond to the sight of the monkey's own hands performing the appropriate hand actions (Perrett et al., 1989d).

Some of the properties of the STS cells described here may well depend on interconnections with the parietal cortex (Seltzer & Pandya, 1978, 1984; Pandya & Seltzer, 1982b). These connections might provide the inputs required for the STS cells to 'ignore' the monkey's own limb movements. It is interesting to consider what kind of information the STS cells require for the observed response selectivity. In the parietal processing the "hand-movement-related" neurons combine the visual and motor/kinesthetic information to produce maximal responses during visually guided hand movements. By contrast, the processing performed within STS suggest that

visual input and motor/kinesthetic signals work antagonistically, the motor/kinesthetic input inhibiting the visual responses to the sight of own arm movements. This inhibition, however, must be very selective. In the experiments where a control object was introduced to the visual field while the monkey's own arm was simultaneously moving in view, the neurons continued responding to the sight of control object motion. Therefore, any inhibition did not prevent all visual processing in the STS cells, but acted selectively (perhaps presynaptically) on the visual motion signal resulting from the own hand movements. Therefore, the inhibition must contain information about the position, trajectory and velocity of the limb motion in three-dimensional space. Kinesthetic information may well be used additionally to give an accurate description about the ongoing motor activity. To match the visual input the motor/kinesthetic signals about hand movements in three-dimensional space must be converted to a retinal co-ordinate system and this necessitates that the dynamic head and eye-position must also be taken into account. As posterior parietal cortex is known to be heavily involved in these functions (see Andersen, 1989), it seems highly possible that this information is used as an inhibitory input and fed either directly or indirectly to the STP cells.

Processing of visual motion which results from eye movements. As described in the introduction neurons in several visual areas have been observed to respond to object motion but not to retinal motion stimulation which is caused by the animals own eye movements. It is interesting that the discrimination against self-produced stimulation is increasingly pronounced at higher levels of motion processing in areas MT and MST (Erickson & Thier, 1991). From this trend one might expect to see the more complex effects of stimulus predictability (of the type we have studied here) only in the anterior STS areas. It should be noted however that throughout the visual system high level areas send back projections down to particular lower areas (Felleman & Van Essen, 1991). These selective back connections from MSTd to MT, V3a and V2

(but not V4) might well mediate the influences of eye motion observed in V1, V2 and V3a by Galletti et al. (1984, 1988, 1990).

In most cases the spontaneous activity of the real-motion neurons in V3A is not affected by tracking movements alone which has been interpreted as suggesting that the eye-motion input selectively inhibits the visual input reaching the real-motion cells (Galletti et al., 1984, 1988, 1990). In this respect the results of the present study are comparable. The movements of the monkey's own hand were not observed to have any effects on the cell's spontaneous activity, and more importantly, the presence of the monkey's own hand in view did not affect the responsivity to simultaneous externally-induced motion. Thus, the inhibition must have acted selectively on the visual input carrying information about the appearance and spatial movements of the monkey's own hand. Indeed, it would be a very maladaptive neural mechanism which shuts down the processing of all external information during self-induced stimulation.

In respect to perceptual experience the responses of real-motion cells offer a physiological basis for the stability of the visual world despite self-induced eye movements. There is not, however, such a clear difference in perception of our own limb movements and the motion of external objects. What, then, could be the functions of the STS cells we have recorded from?

Expectation. Recordings from the parietal cortex, superior temporal sulcus and frontal cortex of monkeys have revealed bimodal cells which give a visual response whenever the body part corresponding to the cell's tactile receptive field was approached by the investigator as though contact would be made (Hyvärinen & Poranen, 1974; Sakata, 1975; Leinonen et al., 1979; Leinonen, 1980; MacKay & Crammond, 1987; Mistlin & Perrett, 1990; Rizzolatti et al., 1981; Gentilucci et al., 1988). As the visual and tactile receptive fields coincide it has been suggested that the

function of these neurons is essentially predictive; i.e. providing information about the impending tactile collision and preparing the animal for an adequate behavioural reaction.

The response properties of the apparently unimodal somatosensory neurons in the STS were found to be very complex (Mistlin & Perrett, 1990). Even though visual stimuli alone did not have any effects on the cell responses it was observed that if the monkey was allowed to see the approaching object before skin contact the responses were reduced. Moreover, not only visual information but also previous experience with the tactile surroundings was capable of inhibiting the effects on the tactile responses. Tactile stimulation resulting from active exploration of a familiar primate chair failed to drive these cells, but as soon as the monkey contacted a novel surface the cells responded vigorously. As a conclusion it was proposed that the responsivity of the tactile STS neurons reflected the "expectation" of the stimulation (Mistlin & Perrett, 1990).

The results of the present study can be interpreted in the context of the effects of expectation as well. When the monkey raised its arm and empty hand into view, the visual appearance of the hand and arm was predictable and hence the cells did not respond, but when an object was placed in monkey's hand out of view and the monkey did not know the visual characteristics of objects, the visual appearance of the compound stimulus (hand + object) was unpredictable and the cells responded accordingly when the compound stimulus came in sight.

If the observed response selectivity was based on this kind of expectation it would mean that some type of matching process must be performed. The mechanisms performing this matching would have to be supplied with information of the visual appearance of the monkey's arm and hand (the STS is known to contain cells selective to hands, Bruce et al., 1981; Perrett et al., 1989d) and this "expected" image

would be compared to the input carrying information about the actual visual stimulation. If they coincided, they would cancel each other. As the cells we recorded from did not modify firing to the sight of monkey's own arm this means that the actual "comparison" was performed on the inputs to the recorded cell or at an earlier stage "upstream".

Overall the results show parallels with the effect of expectation on somatosensory processing in the STS (Mistlin & Perrett, 1990). Unexpected sensory events usually derive from other animals and are therefore behaviourally important. By contrast, predictable sensory consequences of an animal's own actions do not generally require reaction. Cells selectively responsive to the sight of faces and body movements have also been found in the STS. The STS therefore appears to be well suited as a filter for behaviourally and socially relevant sensory events.

CHAPTER EIGHT

STP CELL RESPONSES TO SELF-INDUCED PATTERN MOTION

8.1. INTRODUCTION

The experiments described in Chapter 7 showed that the cell responses in area STP discriminated between the sight of external object movements and the movements of the monkey's own hand. It was discussed that this property might have resulted from the monkey's "expectation" of seeing his own arm and hand. Another possibility was that this discriminative capacity might have resulted from the corollary discharge/proprioceptive input to area STP. It must be emphasized, however, that the contributions of corollary discharge and "expectation" in explaining the observed STP cell responses, are not necessarily incompatible. On the contrary, in some cases corollary discharge/proprioception may be the physiological mechanism which accounts for some "effects of expectation".

The experiments described in this chapter were aimed to clarify two issues raised by experiments of the last chapter. First, is it possible to observe response discrimination in between self- and externally-induced stimulus motion conditions if the visual appearance of the moving stimulus is identical in both stimulation conditions? Even though the cells were thoroughly tested for their apparent lack of selectivity for form, it was possible that the whole discriminative capacity was based on the dissimilarity in visual appearance between the two classes of studied objects (monkey's own arm vs other objects). This type of "pattern recognition" mechanism hypothesis is not at all implausible considering that area STP has repeatedly been shown to contain units with high-level selectivity for visual features, e.g. hands and

faces (Bruce et al., 1981; Desimone et al., 1984; Rolls & Baylis, 1986; Hasselmo et al., 1989; Perrett et al., 1982, 1984, 1985a, 1989c, 1991; Hietanen et al., 1992) although this explanation is unlikely given the employment of a real-looking monkey arm. Secondly, the sight of one's moving limb is a most natural self-produced motion stimulus. Perhaps the discrimination between self-produced and externally-induced stimulation which is so common throughout the nervous system will only be found for such natural and overlearned situations. The question arises, however, is it possible to observe a similar type of response discrimination when the connection between one's own actions and its visual consequences is learned during a relatively short period of time and when it is based on an artificial, not natural, association?

This chapter investigates the extent to which STP cells discriminate against self-produced motion in more arbitrary associations between the monkey's movements and consequent visual motion. For this purpose a monkey was trained to operate a special apparatus that produced visual motion of a grating stimulus. Single unit responses from area STP were recorded and responses to visual motion produced externally, by the experimenter were compared to the responses to visual motion that was produced by the monkey itself.

8.2. METHODS

Behavioural task and training. A monkey was first trained to perform in the LED colour discrimination task (for details, see chapter 5). The monkey was further trained to use an apparatus which was designed to generate motion stimulation under the control of the experimenter or the monkey itself. A description of the apparatus follows.

The apparatus consisted of a vertically oriented handle within a wooden frame. The frame was fitted in front of the primate chair so that the monkey could easily extend its arm out from the chair and turn the handle (Fig. 8.1). The handle (height 20 cm) was situated at the level of the monkey's upper body and was occluded from the monkey's sight by the upper panel of the frame. The movements of the handle were transmitted through a belt to a turntable which was situated out of the monkey's sight, occluded by the side panels of the handle frame. A large diameter, patterned cylinder (see below) was fixed on the turntable and it was monitored by a close-looped video system. By using a video projector (SONY VPH-1041QM) the video image of the cylinder was projected onto the display screen on which the LED lights were located (4 meters in front of the monkey). By turning the handle the experimenter or the monkey could generate a leftward or rightward pattern movement on the screen. Because of the large diameter of the cylinder, the video camera (Panasonic NV-MS1B) could be used to produce a sharp focused video image of the cylinder pattern large enough to fill most of the screen (20 x 30 degrees of visual angle). When the cylinder rotated the video image of the pattern appeared to translate rather than rotate. The construction of the apparatus mechanism also allowed a disconnection between the handle and the cylinder in which case the handle rotation did not result in any pattern movement on the screen.

The upper end of the handle was within a closed compartment, inaccessible by the monkey. This compartment contained two wheels fitted to the end of the handle: one for transmitting the movements of the handle to the turntable and another used for detecting the rotation of the handle. The latter mentioned wheel was covered with 48 evenly distributed silver/black stripes. A light detector system pointed at the wheel detected the changes in light reflectance and was used to generate a short (1 ms) pulse every time a silver stripe was swept across the field of the detector. The minimum angle of handle rotation which could be detected was thus 7.5 degrees. The first pulse in a train of pulses was used to trigger a computer. The rotation of the handle

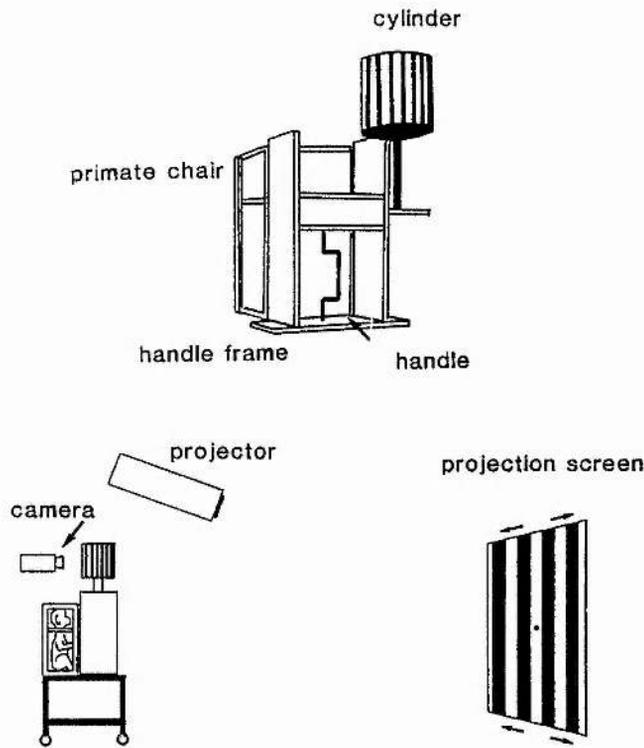


Figure 8.1. A) A schematic drawing of the apparatus used to generate the motion stimulation for the present experiments. B) The experimental set-up. For details, see text.

activated a simultaneous onset of a) a short (100 ms) tone signal, b) the central LED light for 1.0 s and c) data collection of cell activity and eye movements for 1.0 s time period.

As the monkey was highly trained in the LED colour discrimination task, it learnt relatively quickly to rotate the handle in order to activate the LEDs and to have access to reward. The red and green LED lights were presented in random order on different trials under computer control. The monkey performed the LED colour discrimination task at a high level of accuracy (>90%) despite the concomitant pattern movements on the screen. Before the neurophysiological recordings were started, the monkey was trained in this task for 2 months (on average 2-3 training sessions/week), during which time it generated approximately 10,000 trials of pattern motion with concomitant LED fixation light presentation. The training and some early recordings were performed by using a vertically striped white/black pattern on the cylinder. Perhaps because of its high spatial and therefore temporal frequency, this pattern, however, was often found ineffective in eliciting reliable responses in the recorded

cells, and therefore, it was replaced by a irregular low-frequency colour pattern for the majority of the recording sessions.

Testing procedures. After isolating a cell by spike wave form and amplitude its responsivity to visual stimuli was initially tested using a liquid crystal shutter through which the stimuli were presented. On each trial the shutter became transparent for 1.0 s, after a 0.5 s signal tone. It otherwise remained opaque white. The central fixation LED was also visible during the period the shutter was open. First it was established whether the cell response showed any selectivity for stimulus movement over responses to static stimuli. For this purpose, the cell was tested for a sight of moving hand-held objects and the experimenter walking in different directions (left/right, up/down, away/towards) at a range of distances from the monkey (0.2 - 3.5 m). If stimulus motion was observed to affect the responses, selectivity for the direction of movement was tested. Second, the cell responses were tested for form selectivity. Various 3D laboratory objects of different shape, size, colour and texture (human faces and bodies, fruit, tools, boxes, fur etc.) were presented to the monkey by moving them in the cell's preferred and at least in one other (usually 180 degrees from the preferred) direction.

Finally, cells were selected for further testing on the basis of whether or not they responded to leftward or rightward movement at the projecting distance of 4 meters from the monkey. Further testing comprised recording cell responses to the sight of the projected pattern motion generated by the experimental apparatus. If the cell gave reliable and consistent responses to this motion stimulation trials were collected when the pattern was a) moved by the monkey, b) moved by the experimenter, and c) stationary while the monkey moved the handle. In order to measure the cell's spontaneous activity, responses to the sight of the static pattern were collected by leaving the image of the stationary pattern on the screen while the

presentation of the tone and LED light signals was triggered externally. Different conditions were interleaved in counterbalanced order.

Recording procedures and data analysis. Extracellular single unit activity was recorded from one female (J) rhesus monkey (*Macaca mulatta*, wt 4 kg) using standard chronic recording techniques as described in general methods, Chapter 5. In some experiments the filtered cell activity, together with the horizontal and vertical eye position signals and handle rotation signals, were additionally recorded on audio tape using a four-channel FM tape recorder (RACAL) for off-line analysis. This method also provided the most convenient way for inspecting pre-stimulus cell activity for self-initiated trials.

The train of 1 ms pulses generated by the handle rotation was used to assess the velocity of the pattern movement during rotation. For this the pulse train was fed from the audio tape back to the computer and was analyzed with the same program for neuronal spikes analysis. The displacement of the projected pattern while the handle was rotated between adjacent pulses was used to convert the recorded pulse frequency into a pattern velocity.

Horizontal and vertical eye movements were monitored (and recorded during the electrophysiological recording) as described in Chapter 7. Quantitative measurements of cell responses to self-induced and externally-induced pattern motion were obtained by calculating the neuronal spike activity during 250 ms after the stimulus (movement) onset. Cell responsivity to the sight of the static pattern was obtained similarly and was used as a reference level (spontaneous activity) against which the responses to motion stimuli were compared. These data were analysed by using 1-way ANOVA and post-hoc tests (protected least significant difference, PLSD, Snedecor & Cochran, 1980).

After each recording track, frontal and lateral X-radiographs were taken to allow the position of the metal microelectrode to be reconstructed from subsequent histology. The histological procedures were as described in Chapter 5.

8.3. RESULTS

8.3.1. General response properties

51 movement sensitive cells lacking selectivity for form were tested for the possible responsivity for the projected 2D image of the patterned cylinder. Despite the responsivity for moving 3D objects during the initial movement sensitivity testing, 33 cells did not exhibit consistent responses to the projected pattern motion. One reason for this lack of responsivity was found to be the high-frequency stimulus pattern used during the early recordings. However, even after replacing this pattern by a colourful low-frequency pattern, many of the tested units failed to respond to this kind of motion stimulation. Possible reasons for this might have been the relatively large size of the moving stimulus (appr. 20 x 30 degrees of visual angle) or its two-dimensionality.

18 cells responded consistently to the pattern movement and these cells were further subjected to the testing comparing the responsivity between externally-induced and self-induced pattern motion conditions. These cells form the basis for the results presented here.

In the initial movement sensitivity testing 9 cells responded in every direction of object movement in the frontoparallel plane. 3 cells were classified as bidirectional responding to the object movement directed left or right. 6 cells exhibited unidirectional responses, 4 of those to right, 1 up and 1 down. Even though the apparatus had been designed to produce only leftward and rightward movement, two

cells which gave unidirectional responses to object movement along the vertical axis were tested and found to be responsive to the projected pattern movement when the video camera was rotated through 90 degrees to induce vertical (up or down) motion on the screen. The directional preferences of the cell responses during projected pattern movement always matched that observed during initial testing using 3D objects.

Figure 8.2 shows responses of one unit that responded to the large-field pattern movement projected on the wall. The upper part of the figure shows the responsivity in 8 different directions of object movement during the initial directionality testing. The cell was more responsive to motion directed downwards than to other directions of motion or static stimuli. The responses to the projected pattern movement showed the same directional selectivity (lower part of the figure).

8.3.2. Discrimination between responses to externally-induced and self-induced pattern motion

11 out of the 18 cells responding to the motion generated by the apparatus gave statistically stronger responses when the movement was generated by the experimenter as opposed to the self-generated pattern motion. 5 cells of these failed completely responding to the self-induced pattern motion above spontaneous activity, whereas 6 cells exhibited responses to the self-induced motion that were above spontaneous activity, even though statistically weaker than responses to experimenter-induced motion.

Three of the cells which discriminated between externally-induced and self-induced motion were classified as exhibiting directional responses. For one of these cells the only condition which was able to activate the cell above its spontaneous activity was the externally-induced pattern motion in the preferred direction. The two

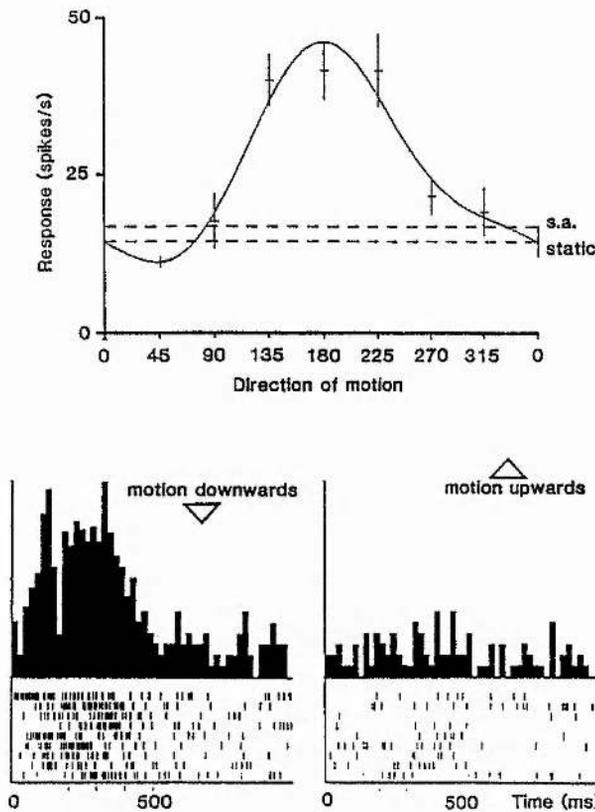


Figure 8.2. Directionally selective responses of one cell (J68_29.25) to object movement and projected large-field pattern movement. Upper part: The cell was tested with 8 directions of object movement in the fronto-parallel plane (0=up, 180=down). The cell responded (mean \pm 1SE) to three directions of object movement (180, 225 and 135, $p < 0.001$) significantly more (PLSD, each comparison $p < 0.001$), than to motion at angles of 0, 45, 90, 315, and 270 or to static control object or spontaneous activity (s.a.). (Overall effect of condition, ANOVA; $F_{8,36} = 18.7$, $p < 0.001$, $n = 5$ in each conditions). The curve is the best fit cardioid function, relating response to direction of movement ($R^2 = 0.68$; $F_{4,35} = 18.2$, $p < 0.001$). Lower part: cell responses to the projected video image of the cylinder used in the experiments. The rastergrams show individual neuronal spikes (short vertical dashes) during post-stimulus time period collected from nine different trials. Poststimulus time histograms (PSTH) show averaged response from nine trials (bin width = 20 ms). The cell responded strongly to the pattern movement directed downwards but failed to respond to similar movement directed upwards (stimulus onset at time 0). The ordinate axes of the PSTHs denote the cell responsivity for 100 spikes/s.

other cells exhibited response discrimination in the cells preferred direction of movement for the stimulation induced by the experimenter compared to self-induced stimulation. Additionally the cells responded at a reduced level to the externally induced non-preferred direction of movement and to the self-induced motion in both directions without showing any response discrimination (Fig. 8.3).

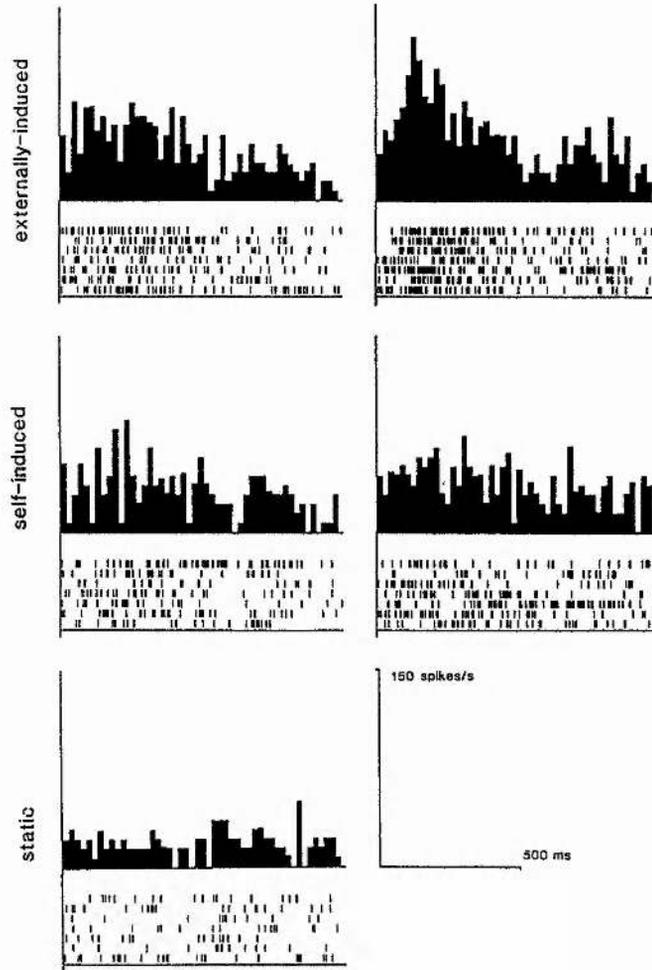


Figure 8.3. Directionally selective responses of one cell (J30_27.05) to externally induced pattern movement. Upper row: response to the externally induced motion to the left and right; middle row: self-induced motion to the left and right; bottom left: response to the static pattern. Externally-induced pattern motion to the right elicited statistically stronger responses than any other stimulus condition ($p < 0.005$ each comparison). The cell responded above spontaneous activity (=static pattern) also to the externally-induced motion directed to the left and to both self-produced directions of motion ($p < 0.02$ each comparison). These responses, however, were graded so that the externally-induced motion to the left did not exceed the self-induced motion to the right ($p > 0.1$), but was anyway stronger than the self-produced motion in this direction ($p < 0.02$). There was no difference in responses between the self-induced conditions ($p > 0.3$). (ANOVA, $F_{4,30} = 17.7$, $p < 0.0005$, $n = 7$ in each condition). Stimulus onset at the beginning of the rastergrams and PSTHs (bin width = 20 ms). Calibration marks on the right bottom corner give the scale of the responsiveness (spikes/s) and time (ms).

Motion velocity. The experimenter tried to match the velocity of the handle rotation with that generated by the monkey. The velocity between individual rotations naturally varied in both cases, but within the range of velocities generated by the experimenter or the monkey, no effect of velocity on the cell responses was observed. Figure 8.4 depicts the results of testing with one cell which responded selectively to

the externally-induced motion and the figure also shows the average velocity curve of the pattern motion across the collected trials.

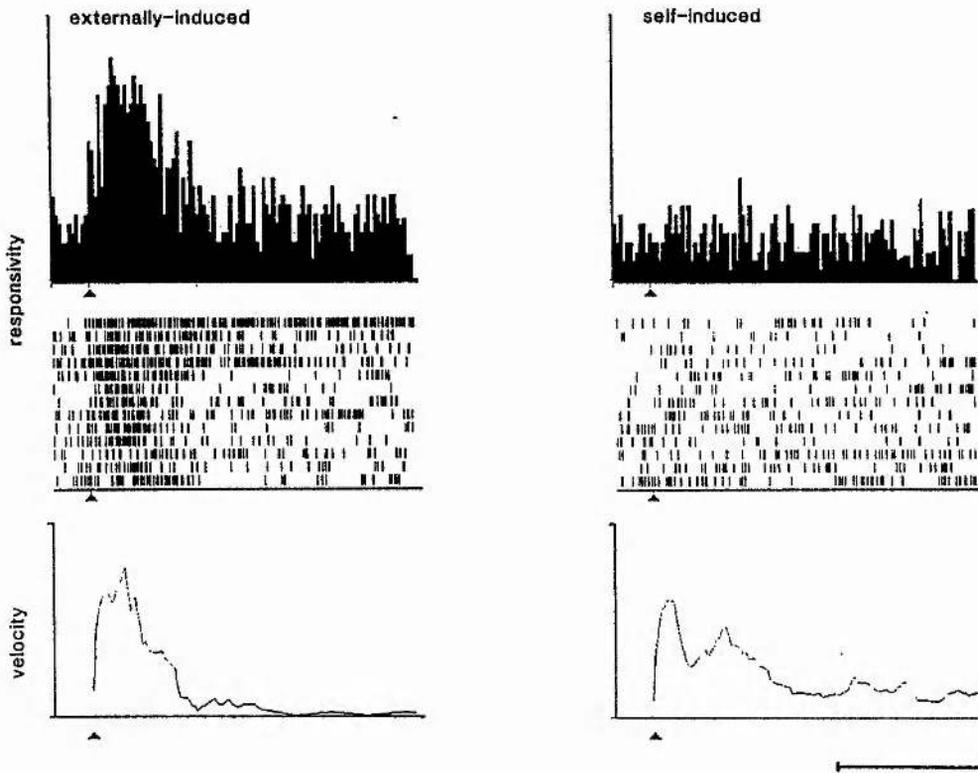


Figure 8.4. One cell (J131_26.11) exhibiting discriminative responses to externally-induced motion. The responses were not directionally selective and the directions of movement are combined for the data analysis. The cell responded in both externally-induced directions of motion above the spontaneous activity and above self-induced motion ($p < 0.0005$ each comparison). (ANOVA, $F_{2,60} = 20.0$, $p < 0.0005$, $n = 18, 28, 17$). The peri-stimulus time rasterograms show neuronal spikes from 13 individual trials and the histograms above them depict the averaged response of these trials (bin width = 20 ms). The curves below the rasterograms depict the average velocity (in degrees of visual angle per second) of the pattern motion across the collected trials. The pattern motion velocity is very comparable in both types of stimulation, especially during the first 300 ms where the difference in strength of responses is maximal. The ordinate axes of the PSTHs denote the cell responsivity for 100 spikes/s. The ordinate axes of the velocity curves denote the velocity for 150 degrees/s. Arrow heads below the time axes denote the stimulus onset. Time scale (1.0 s) shown at the bottom.

Figure 8.5 depicts the cell responsivity and stimulus velocity from four selected individual trials. The figure shows comparable response to one of the slowest and one of the fastest externally-induced pattern motion. Self-induced pattern motion

with comparable stimulus velocity does not activate the cell. The cell is the same as in Fig. 8.4.

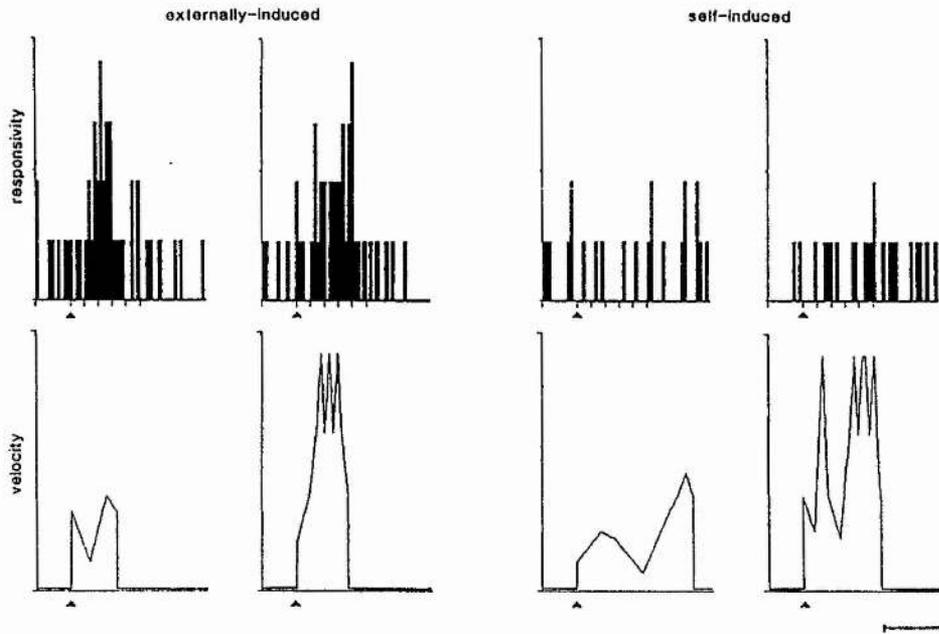


Figure 8.5. PSTHs and stimulus velocity curves from four individual trials in externally- and self-induced stimulus conditions. The cell (same as in Fig. 8.4) responded to externally-induced motion over a wide range of stimulus velocities but failed responding to self-induced stimulation having comparable motion velocities. The ordinate axes of the PSTHs denote the cell responsivity for 200 spikes/s (bin width = 20 ms). The ordinate axes of the velocity curves denote the velocity for 150 degrees/s. Arrow heads below the time axes denote the stimulus onset. Time scale (0.5 s) shown at the bottom.

The effects of motor activity on the cell's spontaneous activity. The testing of 6 of the cells which discriminated between self-induced and experimenter-induced motion included also a condition where the monkey rotated the handle but the handle was disconnected from the turning table and did not, therefore, result in any visual motion. Neuronal data was otherwise collected similarly to the testing during motion stimulation. The cells' responsivity during the handle rotation did not differ significantly from the cells' spontaneous activity in any of the cases.

Motor vs proprioceptive inhibition. A test was conducted in order to have insight into the physiological mechanisms resulting in discriminative responses to self- and

externally-induced motion stimulation. The monkey was encouraged to have a grasp of the handle while the experimenter held the handle stationary. When the experimenter felt that the monkey was holding the handle having its arm otherwise relaxed without any intention to rotate the handle by itself, the experimenter rotated the handle. Collecting such trials so that the monkey held the handle during the externally-generated rotation and was not aggravated by the experimenter's intrusion was not easy, but from one cell a sufficient number of trials were collected. The results (Fig. 8.6) showed that the cell did not respond in this externally-induced condition and indicated that the proprioceptive feed-back was enough to cancel the visual response to the pattern motion.

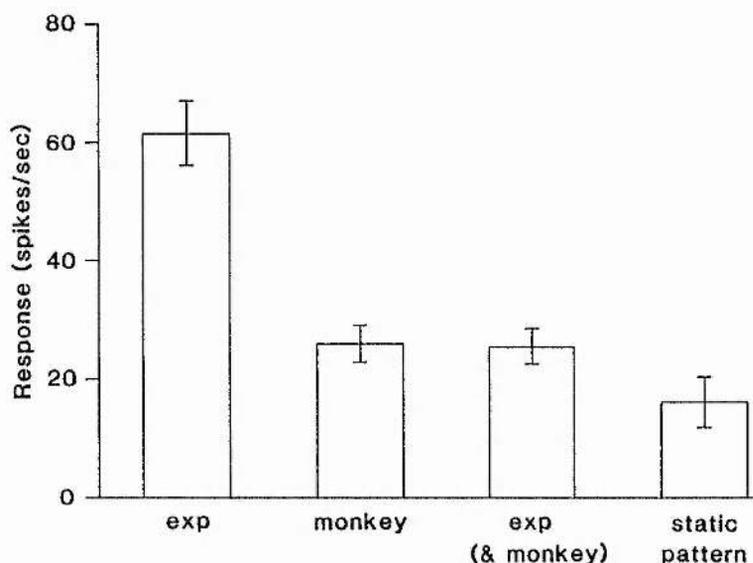


Figure 8.6. Histogram presentation of the mean responses (± 1 SE) of one cell (J137_28.20) to different stimulus conditions. The cell responded to externally-induced pattern motion (exp) stronger than any other stimulus conditions ($p < 0.0005$ each comparison). The responses to the self-induced motion (monkey) or to the externally-induced motion by the experimenter when the monkey passively held from the handle (exp & monkey) did not differ from the cell's spontaneous activity (sight of static pattern, $p > 0.09$). (ANOVA, $F_{3,52} = 23.5$, $p < 0.0005$, $n = 14$ in each condition).

Laterality of the hand used for handle rotation. The monkey was observed to prefer using its right hand in performing the handle rotation, but occasionally it used its left hand as well. During the testing of one cell which was recorded from the right hemisphere the monkey was encouraged to use both its hands and time was spent in

order to collect equal number of responses to self-produced stimuli generated by left and right hand. The cell (Fig. 8.7) responded significantly more strongly to the externally induced motion than to the pattern motion generated by the monkey and the visual responses to self-induced motion were independent of the hand the monkey used for the rotation.

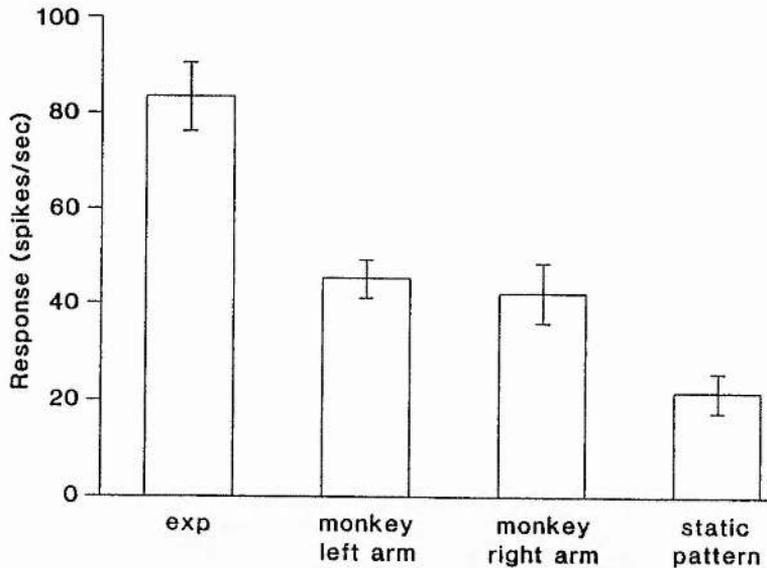


Figure 8.7. Responses (mean \pm 1 SE) of one cell (J30_27.05) that responded significantly stronger to the externally induced motion than to the pattern motion generated by the monkey ($p < 0.0005$). The cell responded also above spontaneous activity ($p < .03$) to the pattern motion generated by the monkey itself, and the responses were almost identical independent of the hand the monkey used for the rotation (ANOVA, $F_{3,43} = 18.3$, $p < 0.0005$, $n = 13, 16, 11, 7$).

8.3.3. Cells responding to self- and externally-induced motion

7 out of the 18 cells tested for responsivity to self- and externally-induced pattern motion exhibited comparable responses in these two stimulus conditions. Figure 8.8 shows an example of the responses of one such cell. As noted above, the experimenter always tried to match the velocity as well as the duration of single handle rotations with those generated by the monkey. During the first half second after the motion onset the visual motion stimulation triggered a response that was very similar independent of the origin of the motion-generation. The cell activity during the self-

generated trials seems to be slightly attenuated as compared to experimenter-induced trials after the first 500 ms, but this probably reflects slight differences in the duration of the handle rotation. This kind of artefact could not, however, explain the observed discriminative responses in cases discussed above as the statistical analysis of the cell responsiveness was always based on the first 250 ms after the motion onset. When selectivity for direction of motion was present (3 cells), the cell responses showed similar directional preference independent of the generator of the movement (experimenter or monkey).

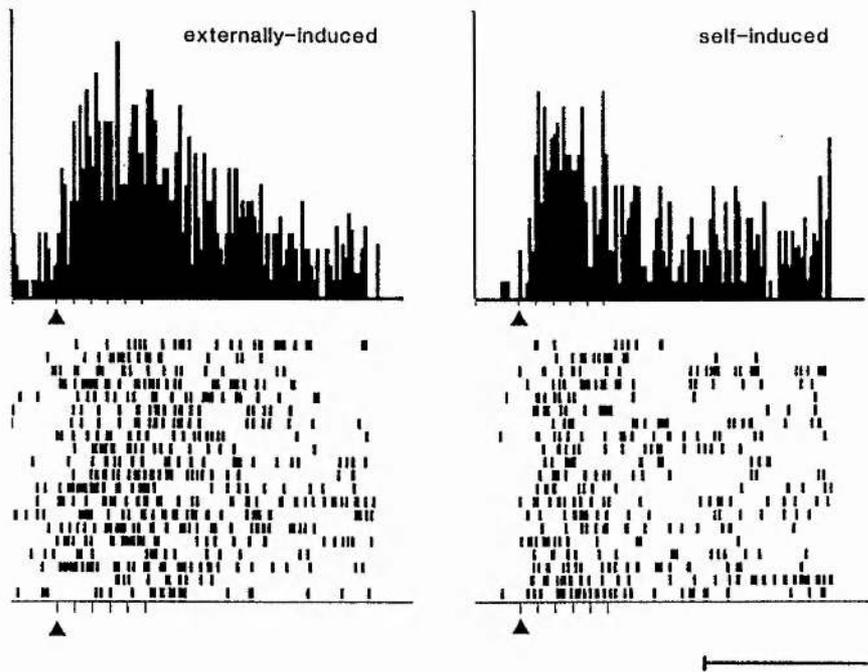


Figure 8.8. An example of the cell (J108_28.98) which responded equally to externally-induced and self-induced pattern motion. Analysis of the cell activity based on the number of neuronal spikes during 250 ms after the stimulus onset revealed that the responsiveness was the same independent of the origin of the motion-generation ($p > 0.5$) and that the responses were significantly stronger ($p < 0.0005$) than the cell's spontaneous activity (not shown). (ANOVA, $F_{2,49} = 11.0$, $p < 0.0005$, $n = 20, 20, 12$). The peristimulus time rasterograms show neuronal spikes from 20 individual trials and the PSTHs above them depict the averaged response of these trials (bin width = 20 ms). The ordinate axes of the PSTHs denote the cell responsiveness for 50 spikes/s. Arrow heads below the time axes denote the stimulus onset. Time scale (1.0 s) shown at the bottom.

As mentioned above, two cells exhibited directional selectivity along the vertical axis and were subjected to the testing for possible discrimination between self- and externally-induced pattern motion by rotating the video camera monitoring

the cylinder through 90 degrees to produce upward and downward motion on the screen. This testing condition was totally unfamiliar to the monkey (for the first of these cells) as the horizontal handle rotation produced now vertical motion on the screen. Both of these cells failed to show discrimination in responses between self- and externally-induced stimulus conditions and gave equally strong responses independent of the origin of the motion.

3 of the cells which failed to show response discrimination between self- and externally-induced stimulus conditions were also tested for the cells' responsivity while the monkey rotated the handle but the cylinder stayed stationary (no visual motion). Unlike the cells which discriminated between self- and externally-induced conditions, the activity of two of these cells was affected by the monkey's motor activity. These cells *increased* their firing rate significantly above the spontaneous level during the handle rotation. For the third cell the motor activity did not change the cell's spontaneous firing.

8.3.4. Relative strength of responses in self- and externally-induced stimulus conditions

A response modulation index (M) indicating the relative responsivity to self-induced and externally-induced stimuli was calculated for the studied cells [$M = 1 - (R_{\text{self}} - s_a) / (R_{\text{ext}} - s_a)$]. Value 0 of the index M would indicate no difference in responses between self and externally-produced stimulus conditions. Values between 0 and 1 indicate progressively stronger responses to externally-produced pattern motion than to self-produced motion and indices between 0 and $-\infty$ indicate increasingly stronger responses to self-produced stimulation than to externally-produced stimulation.

The distribution of the calculated M values for the 18 tested cells is depicted in Figure 8.9. The cells which gave statistically stronger responses to externally-

produced stimulation turned out to have index values > 0.3 , whereas the values of M for the cells failing to show this discrimination are scattered around 0.

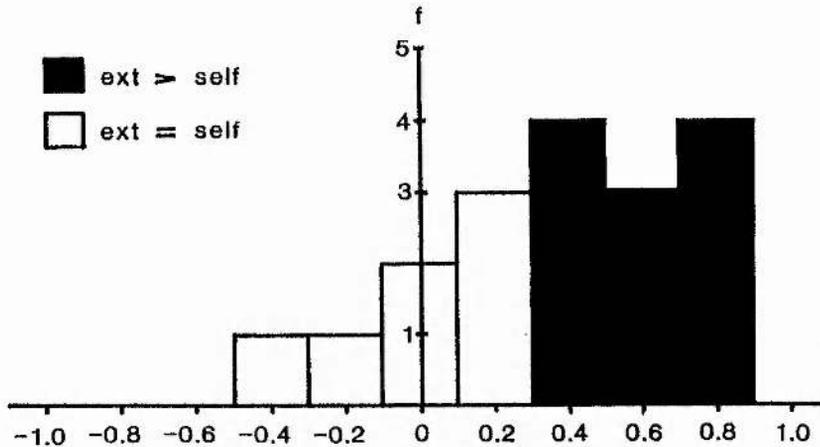


Figure 8.9. Frequency histogram showing the distribution of the M values (see text for explanation) calculated for the 18 recorded cells responding to the projected pattern movement. Black bars indicate the values for the cells which exhibited statistically stronger responses to externally- than to self-induced motion, whereas clear bars indicate values for the cells which failed to show such discrimination.

8.3.5. Eye movements during self- and externally-induced pattern motion

Monitoring of eye movements was essential in ensuring that differences in cell responses to the projected pattern movement generated by the experimenter or by the monkey were not caused by differences in fixation or tracking of stimuli. Eye movement recordings showed (for an example, see Figure 8.10) that despite the pattern motion projected on the screen, the monkey continued fixating on the LED fixation light and generally the eye movement pattern was similar across all stimulus condition types. Cell responses were never found to be linked in time with saccades or fixation onset, but depended on the stimulus condition. For example, in Fig. 8.10 the eye movement recordings indicate that in the externally-induced conditions the monkey was fixating the LED light in every stimulus condition, usually before the trial onset and occasionally 50-150 ms after the stimulus onset. In the self-initiated trials it is obvious that as the monkey knew exactly when the LED light would come on, it tended to be fixating the LED light already at the moment of stimulus onset. The responsivity in the externally-induced stimulus conditions was very unlikely,

however, to result because of the eye movements, as the stronger responsivity on these trials was very clear also during the period of steady fixation. On the other hand, the eye movements after the fixation periods were not correlated with enhanced neuronal activity. Moreover, during the stationary pattern presentation, when the LED was also externally-triggered, there were eye movements present before the fixation, but again, they were not accompanied by neuronal response.

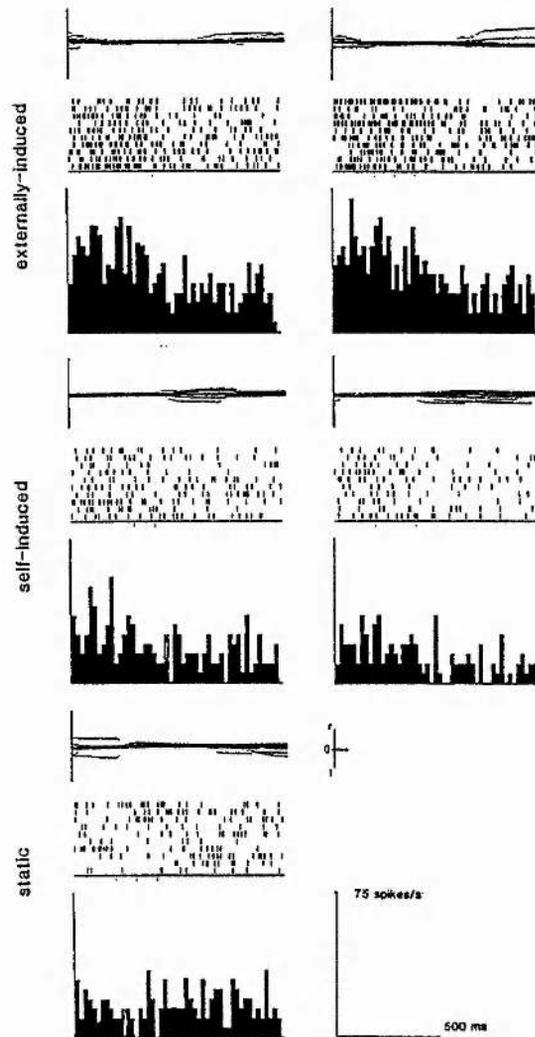


Figure 8.10. Horizontal eye position, poststimulus time rasterograms and PSTHs for a cell (J110_29.49) that responded to externally-induced pattern motion to the left and right significantly stronger above the cell's spontaneous activity (sight of the static pattern, $p < 0.003$). Self-induced pattern motion in either direction did not activate the cell above its spontaneous activity ($p > 0.05$). (ANOVA, $F_{4,43} = 12.1$, $p < 0.0005$, $n = 10$ in each condition). The LED fixation light was activated by the handle rotation at time 0 (the beginning of the time scale) and remained on for 1 second during which time spike activity and eye movement data was collected. Calibration marks on the right bottom corner give the scale of the eye position (± 30 degrees), responsivity (spikes/s) and time (ms).

8.3.6. Location of cells

Histological reconstruction indicated that 15 of the 18 tested cells in this monkey were located in the cortex of the dorsal bank of the superior temporal sulcus (areas TPO and PGa of Seltzer & Pandya, 1978). 9 cells (60%) exhibited selective responses for externally induced motion. Six cells which gave indiscriminate responses to self- and externally-induced pattern motion were also located within this same area.

Even though the recordings were aimed at the dorsal bank of the STS, histological reconstruction indicated that 2 of the studied cells were in the fundus and ventral bank of the STS (areas IPa and TEa of Seltzer and Pandya, 1978). Both of these cells also showed selective responses to the externally-induced motion. One of the tested cells which responded to projected pattern motion but failed to discriminate between externally- and self-induced stimulation was also located in the ventral convexity of the inferotemporal cortex. Figure 8.11 shows the results of the histological reconstruction in the monkey J.

8.4. DISCUSSION

The experiments described in the present chapter were designed in order to find answers to some of the questions arising from the results of the previous chapter. Hence, these two chapters are closely interlinked and several issues raised in the discussion of the previous chapter are equally relevant here and will not be repeated.

Attentional factors. In the neurophysiological experiments where discriminative responses are recorded to two classes of stimuli (especially when the division is between self- and externally-induced stimuli), there is always the possibility that the differential responses simply reflect differences in attention or differences in visual stimulation due to differential eye movements during stimulus presentation. For

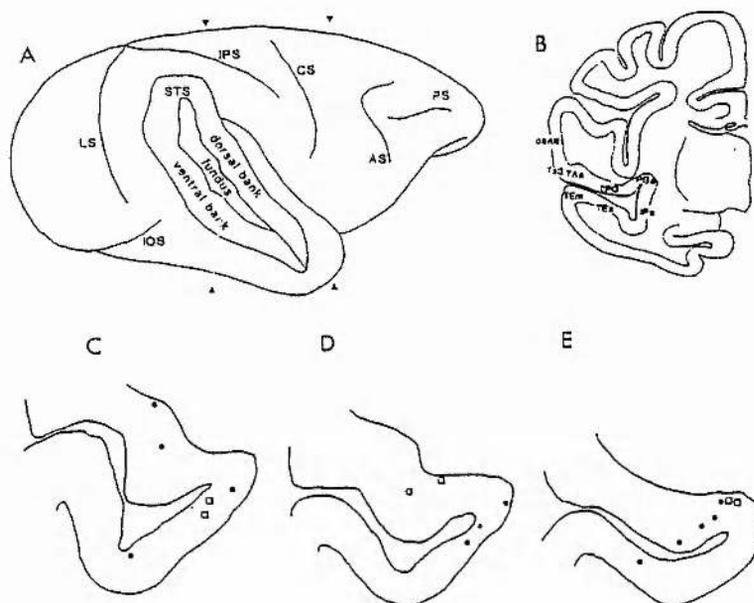


Figure 8.11. A) A lateral view of the right hemisphere of a rhesus macaque brain showing major sulci. Abbreviations: STS = superior temporal sulcus, IOS = inferior occipital sulcus, CS = central sulcus, IPS = intra parietal sulcus, LS = lunate sulcus, AS = arcuate sulcus, PS = principal sulcus. The superior temporal sulcus (STS) is opened to reveal the bottom and both banks of the sulcus. The two pairs of arrows show the interaural plane and a plane 20 mm anterior to it. **B)** A coronal section of the right hemisphere showing the subareas within the STS according to Seltzer & Pandya, 1978. **C-E)** Three enlarged coronal sections of the STS taken at the levels of +6.5 mm, +9.5 mm and +12.5 mm. The position of the recorded cells located between +5 mm and +14 mm along the rostro-caudal extent of the STS. For the illustration, the studied cells from both hemispheres which were located between 5-8, 8-11, and 11-14 are shown in figures **C**, **D** and **E**, respectively. The filled circles mark the location of cells responding selectively to externally-induced pattern movement, and the open squares show the location of cells failing to show this discrimination.

example, the lack of responsiveness to the self-induced pattern motion condition might have resulted from the motion stimulus falling outside the cell's receptive field. This is, however, extremely unlikely simply because the moving pattern occupied a considerable portion of the visual field (appr. 30 x 20 degrees) and the receptive field size of the STP cells is known to be very large, often covering the whole visual field (Bruce et al., 1981). Secondly, the LED colour discrimination task was designed to secure that the monkey directed its gaze straight ahead, in the middle of the moving pattern for both stimulus condition types. The small size of the LED light spot (0.07 degrees of visual angle) necessitated accurate foveating and as the monkey was observed to perform adequately in the discrimination task during both self- and externally-initiated trials, the eye position must have been similar in both cases, in the initial period of fixation. Furthermore, neuronal responses were never found to be

tightly time-locked with the saccades or fixation onsets (see Fig. 8.10). The behavioural task (LED colour discrimination) accompanying both types of motion stimulation supposedly directed the monkey's attention away from the motion stimulation as such, and further ensured that the discriminative responses were not just results of differential attention to externally- and self-induced stimuli.

The effects of previous experience in modifying the STP cell responses. In the previous chapter it was suggested that one of the possible physiological mechanisms responsible for the observed response discrimination was a motor/proprioceptive signal fed from the posterior parietal cortex to area STP and used there to inhibit the responses to the sight of the monkey's own limb movements. This hypothesis is highly plausible because posterior parietal cortex is known to contain neurons maximally active during visual guidance of arm projections (Hyvärinen & Poranen, 1974; Mountcastle et al., 1975; Taira et al., 1990) and heavy anatomical connections exist between posterior parietal cortex and area STP (Selzer & Pandya, 1978, 1984; Pandya & Seltzer, 1982b; Morel & Bullier, 1990; Baizer et al., 1991). The sight of an animal's own limb movements is a natural type of self-produced motion stimulation and it has been suggested that reactions to one's own movements might be innate and "hard-wired" to the neuronal structure (Bullock, 1988, see Chapter 1).

Considerations about whether the observed response properties are based on pre-programmed connectivity or whether they result from plastic processes are relevant for the speculations as to the functional purpose of the described STP cells. One could argue that the lack of STP cell responses to the sight of own limb movements is based on the hard-wired connections between the parietal and STP cortex. On the other hand, it should be remembered that monkeys (as well as humans) undergo through extensive practice in visually guided hand movements and have an enormous experience in observing their own movements. Moreover, even if the rudiments of a neuronal wiring were innate, it must show considerable plasticity as

the signals used for the necessary computations would be changed during the growth process. Finally, if area STP has a role in the processing of externally-produced and "unexpected" information as suggested by Mistlin and Perrett (1990) it would be functionally more useful if the system was capable of plasticity in the adult state and susceptible to relatively short-time experiences.

The results in this chapter clearly indicated that the mechanisms that produced differential STP cell responses to self- and externally-induced stimulus motion in the STP cells, were modifiable by experience. The monkey was trained to perform a task where the connection between its actions and following visual consequences was arbitrary, and definitely nothing that the monkey brain could have been hard-wired for. The majority (61%) of the cells that responded to the visual motion stimulation generated by the apparatus used gave statistically stronger responses when the motion was generated by the experimenter as opposed to similar motion generated by the monkey itself. Some cells failed completely to respond to the self-induced pattern motion, whereas others exhibited weak responses to the self-induced motion. Approximately a third of the cells gave comparable responses to self- and externally-induced motion.

The results with the two cells that were tested by projecting the image of the cylinder so that it was moving along the vertical axis rather than along the horizontal one together with the handle, were particularly revealing. Both of these cells failed to show discrimination in the responses between the self- and externally-induced conditions. These results support the notion that the discriminative capacity had to be based on specific previous experiences in the experimental situation. Two tested cells is not, of course, enough to give any definitive answers. To produce such response properties as those described here, the signal (independent of its origin, see below) that inhibits responses to self-induced motion must be associated with the specific visual input that has repeatedly accompanied a particular motor act in the past. An

interesting experiment would be to study, how quickly these types of structural change take place. It might be possible, for example, to record from one cell for long enough in order to observe a gradual build-up of response discrimination in a case where it did not exist originally.

Physiological mechanisms of the response discrimination. One of the neurons tested in the present experiments was also subjected to the experiments described in the previous chapter. Interestingly, the neuron discriminated between self- and externally-induced motion stimulation in both tests, i.e lacking response both to the sight of monkey's own hand movements and to the self-generated pattern motion. This result makes it unlikely that the lack of responsiveness to the sight of the monkey's own limb was based on the "pattern matching" mechanism whereby the cell would have been supplied with information of the visual appearance of the monkey's arm and hand (area STP is known to contain cells selective for hands, Bruce et al., 1981; Perrett et al., 1989d) and response cancelled if this image matched with the actual visual input.

The results indicated that the spontaneous activity of all the cells which discriminated between self-induced and experimenter-induced motion was not affected by the monkey's motor activity during the handle rotation when there was not any visual motion present. This would indicate that, the mechanism that causes the lack of responsiveness to self-induced motion stimulation, does not work directly on the recorded cells. Rather, the lack of inhibition shows that the mechanism is working specifically on the ascending visual input signal, possibly presynaptically. The same conclusion was drawn from the previous experiments which showed a lack of responsiveness to the sight of own hand movements. There this conclusion was based on the finding that the cells continued responding normally to external movement even when the monkey's own hand was present in view. The idea of presynaptic inhibition is also compatible with the findings from other laboratories that

the spontaneous activity of the visual cells which discriminate between object motion and motion caused by the animal's own eye movements is not affected by eye movements in darkness (Galletti et al., 1984, 1988, 1990; Erickson & Thier, 1991).

The distribution of the response modulation indices presented in Fig. 8.9 showed that the majority of the cells responded more to the externally-produced pattern motion. The negatively skewed distribution may result from the model suggested above, namely that the mechanism which produces weaker responses to self-produced stimulation works presynaptically on the visual input signal. All that the mechanism can do, is to suppress the self-produced motion signal (a total suppression would result in an index value of 1.0), but it can not suppress the cell discharges below the cell's spontaneous activity level (there were no index values greater than 1.0 which would result if responsivity in the self-induced condition was less than the spontaneous activity).

An essential question is the origin and nature of the "self" input that results in the lack of responsiveness to self-induced stimulation. There are several possibilities available: a) a corollary discharge input, b) a proprioceptive input, c) a nonsensory and nonmotor input reflecting a cognitive-mnemonic "expectation" of the stimulus or d) a combination of these three input types. Let us examine the alternatives.

It was shown that when the monkey held the handle while the experimenter performed the actual rotation (and generation of the pattern movement), one cell that was tested this way did not respond in this externally-induced stimulus condition. In this case, as the monkey's arm moved passively, a corollary discharge should not have been emitted either. This would indicate that the corollary discharge is not, or at least is not the only, source of input resulting in the described response discrimination. The results would indicate hence that the recorded cell relied on the proprioceptive feed-back provided the monkey holding the handle during its external

rotation. It is, of course, possible that had other cells been tested, some might have been found to be responsive in this condition. Studies with eye movements have shown that the posterior part of the superior temporal sulcus, area MST (Komatsu & Wurtz, 1988a,b; Newsome et al., 1988) receives a visuomotor corollary discharge signal

The third possibility is that the response discrimination relies on "expectation" of the oncoming visual stimulus. This model would probably include a signal-match mechanism which compares "expectations" with actual sensory stimulation. The existence of this type of matching mechanism has been suggested previously (Freeman, 1979; Hocherman et al., 1981). Let us suppose that area STP is provided with information about the details of the "expected" visual stimulation and that this signal cancels the actual ascending sensory input. The "expectation" must have been built on previous experiences in the experimental situation. Now, the question arises where in the brain, then, a necessary association between a certain motor output and a visual input is formed. Furthermore, this alternative also involves the contribution of corollary discharge, in this case used to trigger the "expectation" signal whenever a particular motor act is realized. One problem with this hypothesis is that according to the model the self-generated handle rotation without any visual motion should produce a response because now the "expectation" does not match with the actual ascending visual signal. Six of the cells which exhibited discriminative responses to self-produced stimulation were tested in this condition, but none of them responded.

Several brain areas have been shown to exhibit nonsensory and nonmotor neuronal signals that have been suggested to reflect "anticipatory" responses to external events. Such responses has been found in prefrontal (Sakai, 1974; Niki & Watanabe, 1979; Joseph & Barone, 1987), premotor (Mauritz & Wise, 1986), parietal (Mackay & Crammond, 1987) and cingulate (Niki & Watanabe, 1979) cortices and subcortically in the nucleus caudatus (Rolls et al., 1983; Hikosaka et al., 1989). In

these cases the anticipatory responses are dependent on the specific context of experimental behavioural paradigms used and they have been suggested to prepare the animals for the next stages in a sequential behaviour.

Rolls et al. (1983) has described response properties of single-units in the anterior parts of the nucleus caudatus that are similar to those reported in here. Generally, the responses of neurons in the anterior striatum are not tightly linked with specific sensory inputs or motor outputs, but rather reflect the significance of external events in preparing the animal to initiate behavioural responses. Many of the response properties are present only in a behavioural testing paradigm where the animal has had a possibility to form "expectations" of the sequence of external events based on its extensive previous experience in performing in a particular task. For example, Rolls et al. (1983) reported that in a task where the animal was required to perform a visual discrimination for stimuli presented from behind a shutter, the shutter opening was observed to elicit a clear response from the striatal cells. This response was not, however, a visuosensory response to the discriminanda. This conclusion was based on the observations that an additional visual or auditory cue prior to the shutter opening reduced the response latencies radically. Instead, it was suggested that the response was elicited by the opening of the shutter that worked as a cue for the animal to prepare itself for the visual discrimination task. Particularly interesting were the results from the tests where the animal was able to initiate the trials itself. In this condition there was no response to the opening of the shutter, even though the sensory event was exactly the same. There is, however, one essential difference between these caudate responses and the reported STP responses that must be considered. In the present experiments the occurrence of the neuronal response was totally dependent on the special type of visual stimulation (i.e. motion, which in some cases had to be even in a certain direction) and reflected, hence, strictly sensory processing of the visual input.

The other cortical areas mentioned above showing "anticipatory" activity resemble area STP in the sense that these areas, too, are more directly involved in purely sensory or motor processing as compared to the caudate nucleus. Rolls et al. (1983) has suggested that the function of striatum is to relay the results of sensory (or "cognitive") processing performed in cortical areas to the motor systems. This hypothesis offers appealing explanations as to the functions of STP cortex. It can be postulated that one of the functions of area STP is to separate externally-caused and "unexpected" sensory inputs from those that result from the individual's own actions and to relay the information from the external events further, for example, to the striatum in order to prepare the animal for necessary behavioural responses. Anatomical connections exist between area STP and the striatum (Van Hoesen et al., 1981). Even though the motion stimulation did not have any behavioural significance to the monkey in the present experiments, it probably would in the natural environment. The present results further strengthen the hypothesis proposed by several studies (Bruce et al., 1981; Luh et al., 1986; Mistlin & Perrett, 1990; Gross, 1991) that area STP monitors the visual environment for unexpected events.

CHAPTER NINE

STP CELL RESPONSES TO VISUAL IMAGE MOTION DURING OBJECT- AND SELF- MOTION

9.1. INTRODUCTION

It has long been recognized that the visual system must distinguish object-motion characteristics which help define object identity and actions of other animate objects from self-induced visual motion which helps define the actions of the observing organism (Helmholtz, 1911; Von Holst & Mittelstaedt, 1950; Gibson, 1966). In most cases the deformation of the retinal image due to ego-motion is qualitatively different from that caused by object motion. As an observer moves in the world, the locomotion will be accompanied by flow in the optic array which is specific to the type of movement. For example, approach is accompanied by centrifugal expanding of the texture elements in the world whereas retreat is specified by inward streaming of optical texture elements towards the point from which one is drawing away. The characteristic nature of optic flow in signalling different types of self-motion led Gibson (1966) to suggest that vision is not only exteroceptive, providing information about events extrinsic to the animal, but also proprioceptive for obtaining information about organism's own actions.

The perception of object-motion has been suggested to comprise two components: observer-relative and object-relative motion cues (Bruce & Green, 1990). A pure form of observer-relative motion can be achieved in darkness by witnessing movements of a spot of light. In this condition the perception of external object-motion is based on image displacement across the retina and smooth pursuit

eye movements in tracking the moving object (Wallach et al., 1982). The observer's own egocentre is used as a frame of reference in attributing the motion. In light, however, object-relative (or environment-relative) cues start to contribute to the perception of object-motion and, in fact, tend to dominate observer-relative cues. This is evident, for example, from the illusionary perception of movement ("induced movement") of a stationary spot surrounded by a moving frame (Reinhardt-Rutland, 1988). Object-relative motion is based on the configurational changes in the retinal image (Wallach et al., 1982).

Now, the interesting question for a neurophysiologist is, of course, whether the self-motion and object-motion types of image motion characteristics can be shown to be processed by separate visual systems, and if so, what mechanisms allow the differentiation. Neurophysiological single-unit recordings with rabbits, cats and birds have provided evidence that the accessory optic system (AOS) is a likely candidate for processing whole-field motion (Simpson, 1984; Soodak & Simpson, 1988; Frost et al., 1990). At the cortical level the dorsal part of area MST (MSTd) in primates has also been shown to contain cell populations with response properties suggesting a functional role in visual self-motion detection (Tanaka et al., 1986; Saito et al., 1986; Tanaka & Saito, 1989; Duffy & Wurtz, 1991a). Like neurons in the AOS, a large fraction of the MSTd cells prefers the movement of a wide field of elements to movement of a small object.

Neurons particularly suitable in signalling object-motion in the environment have been described in the optic tectum of birds (Frost et al., 1990), suprasylvian area of cats (Von Grünau & Frost, 1983), the superior colliculus (Bender & Davidson, 1986), area MT and the ventral part of area MST (Allman et al., 1985; Saito et al., 1986; Tanaka et al., 1986; Sugita et al., 1990) in monkeys. These cells have a receptive field organization which consists of two (figure-background) directionally specific mechanisms having opposite directional preferences. In the receptive field

center the cells exhibit responses to a local stimulus movement in a preferred direction against a stationary background. The responses are facilitated if the background is moved simultaneously in the opposite direction of motion but if the background is moved in phase in the same direction and speed with the local stimulus the responses are inhibited.

It should be noted, however, that in natural conditions the visual attributes typifying self-motion and object-motion are far from being clearly separated. Let us consider the perception of a moving object in a three-dimensional environment. The observer-relative motion cues, i.e. retinal image displacement and eye movements, are identical independent of whether the image motion on the retina results from object-motion or from the movements of the observer (self-motion). Moreover, it is not only objects moving in the environment that evoke cues about object-relative motion. Self-motion in any plane creates local discontinuities in the velocity field at the edges of objects which are located between the observer and the background, and a lateral displacement of head, for example, results in relative displacement of objects at different distances (motion parallax). Interestingly, Roy and Wurtz (1990) have found MST neurons that are responsive to motion in the fronto-parallel plane code the direction of movement as well as the depth of motion from disparity cues. When stimulated with random dot displays the neurons responded, for example, when the "foreground" (i.e. in front of the plane of fixation) moved to the left or when the "background" (a stimulus behind the plane of fixation) moved to the right, or both of these movements. Roy and Wurtz have argued that these MST neurons would, therefore, be very effective in signalling the direction of self-motion.

Unlike the response properties of the motion sensitive units in areas MT and MST, the cells in the most anterior parts of the superior temporal sulcus, area STP (superior temporal polysensory area), have not been subjected to such extensive studies. This area receives a direct anatomical projection from area MST (Boussaoud

et al., 1990) and single-unit recordings have shown that individual STP units do respond to object motion and some exhibit directional selectivity (Bruce et al., 1981, Perrett et al., 1985b; see Chapter 6). The specific functions of area STP in visual motion processing are, however, largely unresolved. A small minority of the units seem to combine motion sensitivity with high-level form sensitivity producing selective responses, for example, to the sight of body movements in a certain direction (Perrett et al., 1985b, 1989c, 1990a,b). Most of the motion sensitive units, however, do not show selectivity for stimulus form.

The present experiments were designed to study the response properties of visual motion sensitive STP units to object-motion and self-motion in natural conditions. Instead of using display images of moving objects or whole-field images mimicking visual stimulation during self-motion, the cells were subjected to experiments where responses were measured to image motion which resulted from movements of real objects in space while the monkey was stationary and to the image motion of the same object which resulted from the translatory movement of the monkey itself.

The experiments addressed two intermingled questions simultaneously. As area MST, which has been suggested to process wide-field motion information that would result from animal's locomotor movements in the environment projects directly to area STP, it would be reasonable to expect to find similar responses in area STP as well. The two previous chapters, however, presented results where the motion sensitive cells in STP were shown to discriminate between visual motion resulting from externally- and self-produced actions. Perhaps these same discriminative response properties also apply to visual image motion resulting from object-motion and self-motion of the whole body. If one of the functions of the area STP is, as suggested previously, to process and filter "unexpected" information originating from external sources, then one would expect to find the STP cells responding to

movements of objects in the environment but lacking responses to image motion resulting from the animal's self-motion in the environment. Secondly, the contribution of observer-relative and object-relative motion cues in driving the STP cell responses to object-motion was examined. This is a particularly important issue in the context of the present experiments, i.e. when responsivity to object- and self-motion is studied. As mentioned above, object-motion and self-motion result in identical observer-relative motion cues. If response discrimination of object-motion and self-motion is found, it would suggest that the cells are coding object-motion in object-relative terms and the response discrimination could be explained solely in terms of differences in retinal stimulation. On the other hand, if the cell responses can be shown to be driven by observer-relative motion cues, then the possible discrimination between object-motion and self-motion must be based on extraretinal mechanisms. The importance of these issues in revealing the hierarchical organization within the multiplicity of visual motion processing areas will be discussed.

9.2. METHODS

Testing procedures and data collection. After isolating a cell its responsivity to static and moving visual stimuli was tested using a liquid crystal shutter as described in previous chapters.

After the cell's responsivity for stimulus movement was established, neuronal responses were collected to the sight of image movements and static images in a testing protocol whereby the image movement was produced either by moving the object (while the monkey was stationary), by moving the monkey (while the object was stationary) or by moving the both (see below). The monkey's movement (self-motion) was produced by moving the primate chair in which the monkey was sitting during the experiments. The primate chair was located on top of a movable trolley

which had four wheels each free to rotate about an axis orthogonal to the draw motion. This arrangement made it possible to move the monkey smoothly either to the left and to the right or forwards and backwards.

A testing protocol was comprised of the following stimulus conditions which allowed inferences to be made about cell responsivity to object-motion and self-motion and what type of object-motion cues was processed by the STP cells (see Fig. 9.1): a) moving an object in the cell's preferred direction (monkey stationary), b) moving the monkey in the opposite direction (object stationary), c) moving the object in the cell's preferred direction while moving the monkey (in parallel) in the same direction (no relative movement between the monkey and the object), d) moving the object in the cell's preferred direction while moving the monkey in the opposite direction, and e) presenting a static object to a stationary monkey. In some experiments stimulus conditions a), b) and c) were also carried out in darkness by using an illuminated object as a stimulus object. The selection of individual trials during a testing protocol in pseudorandom order was controlled by a computer programme.

Responses were collected by presenting the stimuli through a liquid crystal shutter for 1 second, as described in Chapter 5. The onset of the stimulus movement or the monkey's movement was synchronized with the onset of the tone signal which preceded the shutter opening by 500 ms, and the movement continued for the whole period of time while the shutter was open. The moving (or static) stimulus used in majority of the tests was the experimenter's head and upper body. To produce a moving stimulus the experimenter translated his head at a distance of approximately 1 m in front of the monkey. With this proximity, the monkey could not see the experimenter's lower body through the shutter aperture. This ensured that the appearance of the stimulus was the same in object-motion and self-motion conditions.

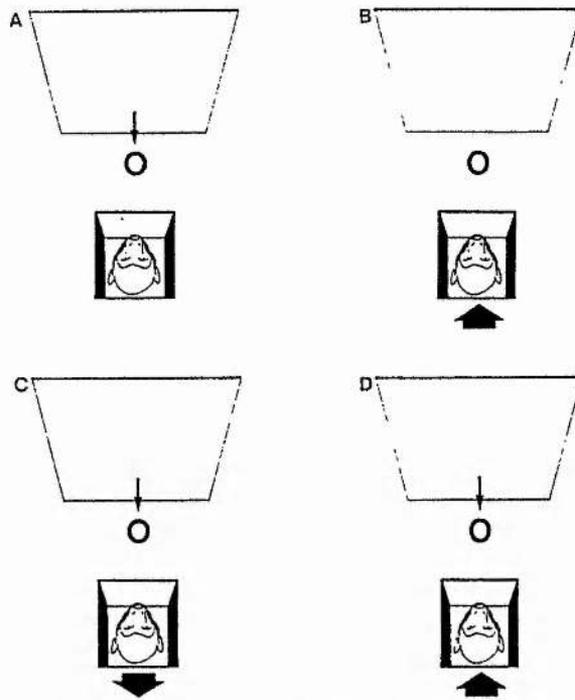


Figure 9.1. An example of the different stimulus conditions used for testing a cell which prefers approaching movement of an object (O). Small arrows indicate the direction of object movement and big arrows indicate the movements of the monkey. An absence of an arrow indicates a stationary object/monkey. Figure **A** depicts object-motion and figure **B** self-motion. In conditions **A** and **B** the object produces object-relative motion cues relative to its background and observer-relative cues relative to the monkey. In condition **C** the observer-relative cues have been eliminated by moving the monkey together with the object in the same direction (so that the object is not coming closer to the monkey) but the object-relative cues are still present as the object moves in relation to its background. Moving the object and monkey in the opposite directions as indicated in condition **D** results in "enhanced" object- and observer-relative motion cues.

In the testing condition c) this arrangement also provided a simple and accurate way to meet the requirements for the elimination of the relative movement between the monkey and the object while still both moving as the experimenter could easily move the trolley and keep the distance between his body and the monkey unchanged. In other conditions the trolley was moved by an assistant with a comparable speed to that of the stimulus (experimenter) movement. During the experiments which were carried out in darkness an illuminated rod (length 30 cm, width 4 cm) held by the experimenter was used as a stimulus object. The velocity of the stimulus motion or monkey's self-motion was approx. 1 m/s in all the experiments.

A video film was also prepared in order to study cell responsivity to relative motion cues. An object (a human head) was filmed against a light background with a

video camera (JVC BY-110E) and recorded on 3/4 inch U-matic videotape. This film was processed using a video effects unit (Fairlight CVI) in order to generate a regular dot field background for the object. Several types of relative motion stimuli were prepared (see Results). The processed video film was transferred onto a laser video disc (RLV Mk II, Optical Disc Corp.), replayed with a video disc player (Philips VP406 LaserVision Disc Drive) and projected onto a display screen (using a Sony colour video projector VPH-1041QM). The testing involved computer controlled selection of desired stimuli and "unblinking" (switching on with 0 ms delay) the video signal to the projector for a 1 s stimulus presentation.

Recording procedures and data analysis. Extracellular single unit activity together with horizontal and vertical eye movements was recorded from four rhesus monkeys (*Macaca mulatta*, two females and two males, wt 4-8 kg) using standard chronic recording techniques as described in general methods, in Chapter 5.

Quantitative measurements of cell responses to image motion caused by object-motion and self-motion and to static stimuli were collected, based on the neuronal spike activity during a 250 ms time period collected 100 ms after the stimulus onset. The data were usually collected from five stimulus presentation cycles in each condition and these data were analysed by using 1-way ANOVA and post-hoc tests (protected least significant difference, PLSD, Snedecor & Cochran, 1980).

After each recording track, frontal and lateral X-radiographs were taken to allow the position of the metal microelectrode to be reconstructed from subsequent histology. The histological procedures were as described in Chapter 5.

9.3. RESULTS

9.3.1. General response properties

19 movement sensitive cells were tested for their responsivity to the image motion resulting from object-motion and from self-motion. In the testing for directional selectivity 4 cells turned out to respond in every direction of object movement in the horizontal plane. The remaining 15 of the cells were classified as unidirectional; 14 of these responded to object movement in one direction significantly stronger than in the other directions and 1 cell responded comparably in three directions of movement but failed to respond in a fourth direction. The distribution of preferred directions and response latency of these cells was similar to those described in Chapter 6. The cell responses were occasionally studied for their selectivity for stimulus velocity, but never observed to be dramatically affected within the range of approx. 0.5-3.0 m/s.

9.3.2. Responsivity during object motion and self-motion

16 out of 19 cells exhibited statistically stronger responses to the sight of an object movement than to the sight of visual motion that resulted from the monkey's self-motion. In fact, for the 16 cells the responses to an objectively stationary object during self-motion never exceeded those observed during the presentation of a static object to a stationary monkey. Figure 9.2 depicts the results of experiments with one cell which discriminated between object-motion and visual self-motion. The cell exhibited a strong response to the sight of an object which moved with a speed of approx. 1 m/s away from the monkey. However, the cell failed to respond when the object was stationary and the monkey was moved away from it with the same speed.

Three out of the nineteen cells failed to show any discrimination between object-motion and visual self-motion in their responses, but exhibited comparable responses in both conditions (see Fig. 9.3). These results also provide evidence that

the response discrimination between object-motion and self-motion as described above was not due to unstable recording during the movement of the primate chair. The distribution of preferred directions of the cells which exhibited response discrimination between object-motion and self-motion did not differ from that of all the motion sensitive cells.

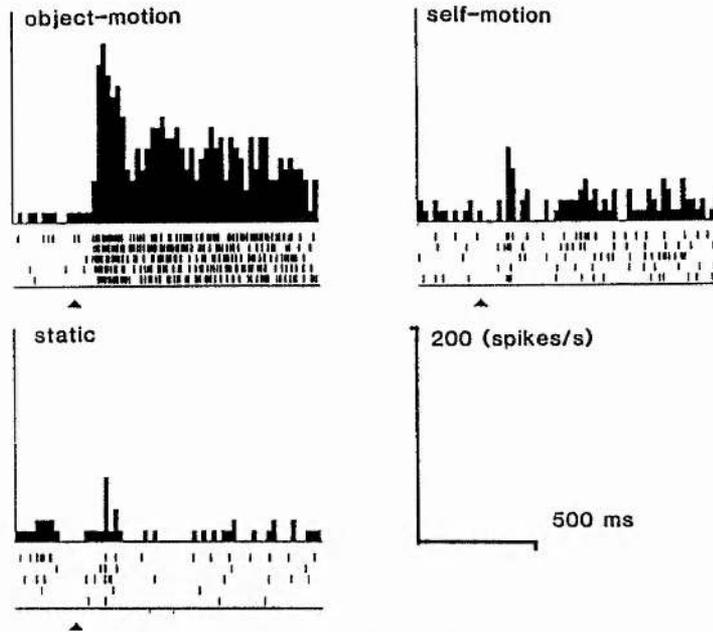


Figure 9.2. A cell (J76_29.51) responding to the sight of a retracting object, but failing to respond to a visual motion which was achieved by moving the monkey (the primate chair) away from a static object with the same speed. The response to the object motion was significantly stronger (PLSD, $p < 0.0005$) than the responses during self-motion or during static object presentation. There was no difference in responses in between the two latter stimulus conditions (PLSD, $p > 0.3$). (ANOVA $F_{2,12} = 124.4$, $p < 0.0005$, $n = 5$ in each condition). The peristimulus rasterograms present the neuronal spike activity collected from five interleaved trials and the histograms above each show an averaged activity from these trials (bin width = 20 ms). The arrow heads below the time axes denote the stimulus onset. Calibration marks on the right bottom corner scale the responsiveness (spikes/s) and time (ms).

9 out of the 16 cells which discriminated between object-motion and self-motion were also tested by moving the object in the cell's preferred direction while the monkey was moved simultaneously in the opposite direction. So, for example, if a cell was found to be responsive to object movement to the left (and not responding when the object was static but the monkey was moved right), the cell was tested with the object moving to the left while the monkey was moved to the right at the same time. 7 out of the 9 cells tested this way exhibited indistinguishable responses to those

obtained during object-motion only (Fig. 9.4). The responsivity of one of the remaining 2 cells was significantly lower than response during object-motion when

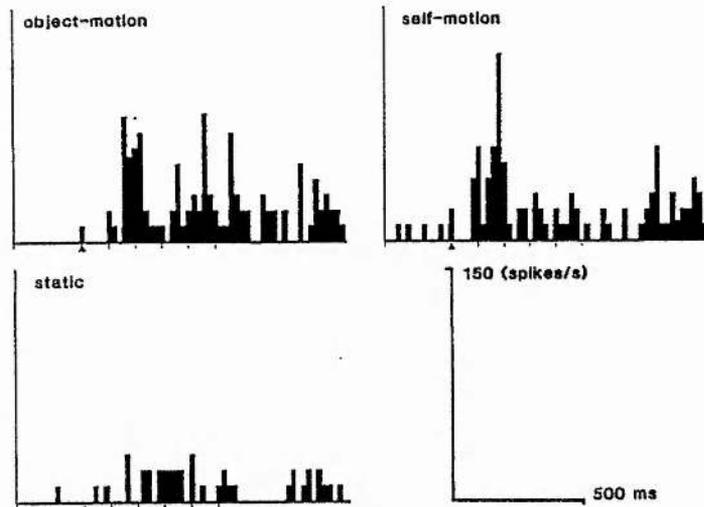


Figure 9.3. A cell (J113_29.93) exhibiting responses both to the sight of an object moving towards the monkey and to the sight of the same stationary object when the monkey was moved towards it. Both conditions resulted in responses that were stronger than the responses in a static object presentation condition ($p < 0.01$). (ANOVA, $F_{2,12} = 6.6$, $p < 0.02$, $n = 5$ in each condition). Peristimulus time histograms (PSTH) show the average activity collected from five trials in each condition (Bin width = 20 ms). Arrow heads below the time axes denote the stimulus onset. Calibration marks on the right bottom corner scale the response activity (spikes/s) and time (ms).

the responsivity estimation was based on the used data sampling period (250 ms after 100 ms latency from the stimulus onset). A longer sampling period (500 ms), however, produced comparable responses between these two conditions for this cell, too. The other cell showed a reverse pattern. The cell gave a comparable phasic burst for object-motion independent of monkey's own movement, but exhibited attenuated responsivity after the phasic response for object-motion during concomitant self-motion.

9.3.3. Observer-relative and object-relative motion

The contribution of observer-relative and object-relative motion cues to the cell responses was studied by recording cell responses in various stimulus conditions as explained in the methods. Object motion in the light provided both visual motion cues, i.e. observer-relative and object-relative cues ("observer/object-relative"

condition, see below). Motion of an illuminated object in darkness eliminated the effects of object-relative cues, but left the observer-relative cues intact ("observer relative only")

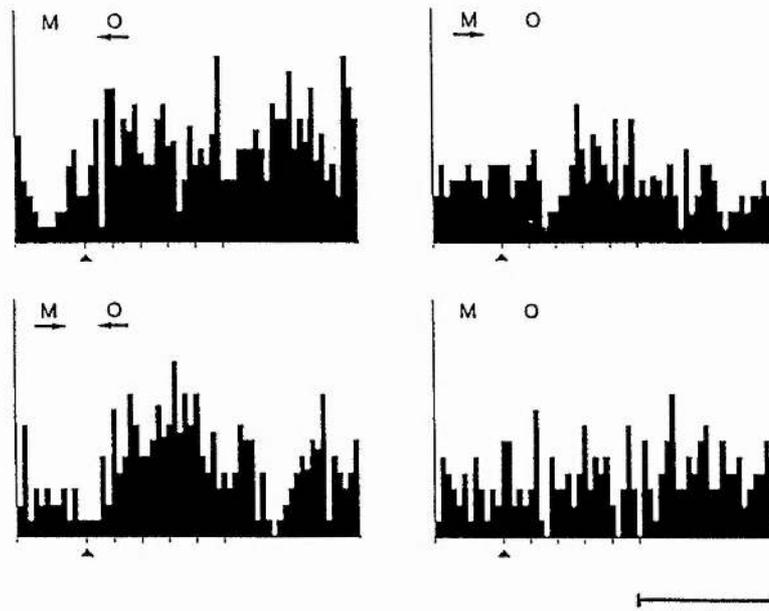


Figure 9.4. PSTHs showing visual responses of a directionally selective cell (J75_33.44) to object-motion, self-motion, object-motion during self-motion, and to the sight of a static stimulus. The panels in the upper row show that the cell responses to the sight of an approaching object (O, the arrows show the direction of motion) while the monkey (M) was stationary were significantly stronger than when the monkey was moved towards a stationary object ($p < 0.04$). The cell responded to approaching object-motion despite the concomitant self-motion towards the object (bottom left) comparably to the condition when only the object was moving ($p > 0.9$). The panel on the bottom right corner illustrates the cell responses to the sight of the object in a static stimulus presentation condition. (ANOVA $F_{3,16} = 4.0$, $p < 0.03$, $n = 5$ in each condition). The ordinate axes of the PSTHs denote the cell responsivity for 150 spikes/s. Time scale (500 ms) shown at the bottom. Small arrow heads below the time axes denote the stimulus onset.

condition). Finally, object motion in the light together with movement of the monkey in the same direction so that there was no relative movement between the monkey and the object present allowed object-relative cues to be isolated ("object-relative only" condition).

13 cells (out of the total 19) were tested both in the "observer/object-relative" and in the "object-relative only" stimulus conditions. 10 cells failed completely to respond in the "object-relative only" condition. Figure 9.5 shows an example of this

type of a cell. The cell responded strongly to the sight of a retracting object. Now, if the cells was driven by the object-relative motion cues (uncovering of the background texture elements, for example) it should have responded also when the monkey was moved together with the object while keeping the distance between the object and the monkey invariable. The results indicate, however, that the cell was driven by motion relative to the observer.

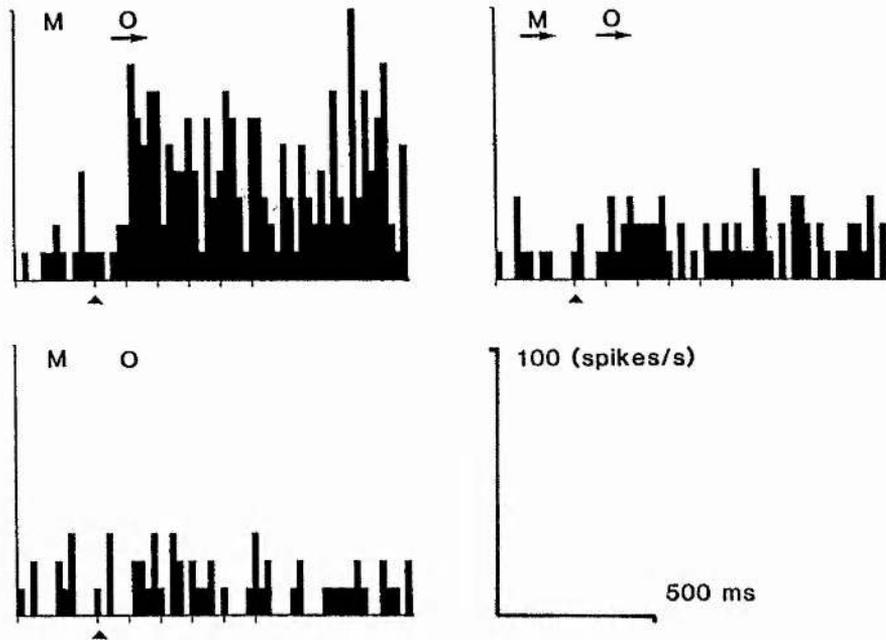


Figure 9.5. A cell (J104_28.76) responding only to observer-relative object-motion. The PSTH on the upper left depicts visual responses to the sight of a retracting object. This stimulus condition elicited a response that was significantly stronger than responses when the monkey and object were stationary (PSTH on bottom left, $p < 0.002$). The cell did not respond, however, when the monkey and the object were moved together so that there was no relative movement between the monkey and the object, despite the presence of the object motion relative to background. (PSTH on upper right, $p > 0.6$). (ANOVA, $F_{2,12} = 9.3$, $p < 0.005$, $n = 5$ in each condition). Calibration marks on the right bottom corner give the scale of the responsivity (spikes/s) and time (ms).

One of the cells which failed to respond in the "object-relative only" stimulus condition was also tested in the darkness. Now, if the cell was driven by the observer-relative motion cues, the elimination of the background should not abolish the responsivity to the object motion in darkness. Figure 9.6 depicts the results of the testing with this particular cell. It shows that even though the responsivity was affected by the general light level so that the cell's spontaneous activity (not shown)

and response during self-motion was reduced in darkness the cell still continued responding in the object-motion condition.

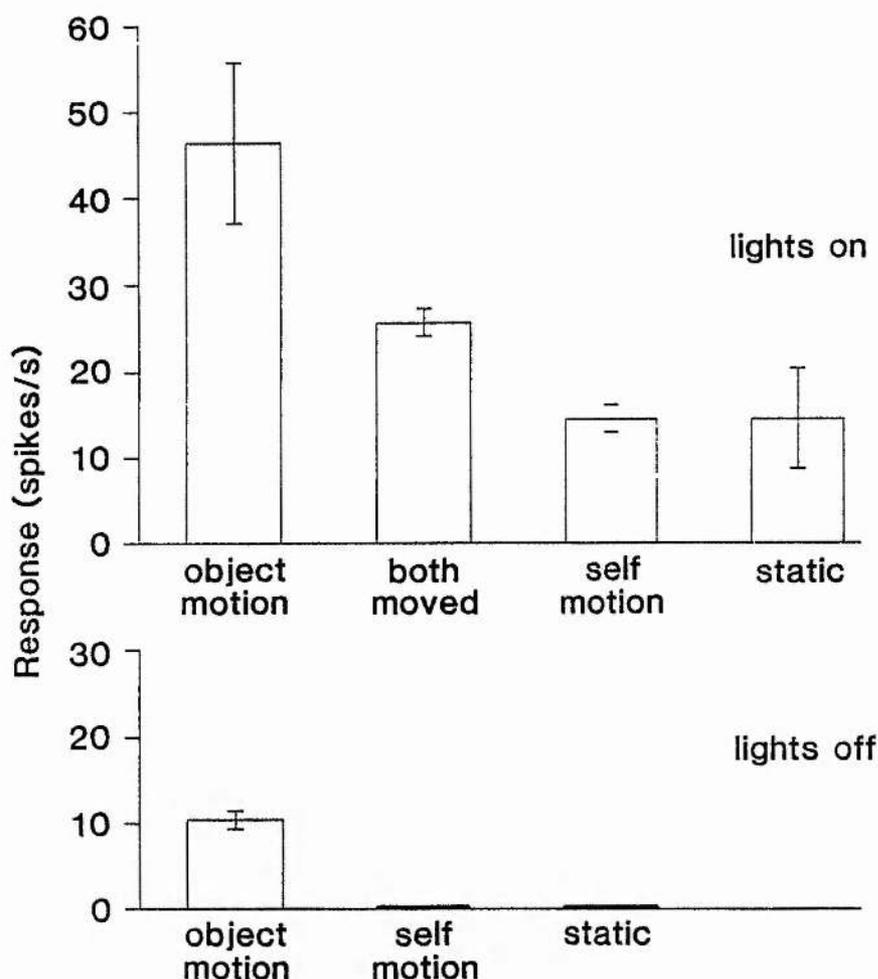


Figure 9.6. A histogram presentation of the mean (± 1 SE) responsivity of one cell (J63_27.58) in different stimulus conditions. The upper histograms depict the results of testing in light and show that the cell responded to object movement to the right significantly stronger than when the object was stationary and the monkey was moved to the left ($p < 0.001$) or when they both were moved to the right so that the relative position of the monkey and the object was kept constant ($p < 0.02$). The cell did not respond above spontaneous activity (=static object) in either of these latter mentioned conditions. (ANOVA, $F_{3,16} = 7.3$, $p < 0.004$, $n = 5$ in each condition) The spontaneous activity of this particular cell was abolished when the room lights were turned off (no spikes occurred during five cycles of the data sampling period). However, the cell still exhibited consistent responses to the sight of an illuminated rod moving to the right, but did not respond at all when the monkey was moved to the left while the object was kept stationary (ANOVA, $F_{2,12} = 112.7$, $p < 0.0005$, $n = 5$ in each condition)

Three cells, however, exhibited responses in the "object-relative only" condition that were indistinguishable from those during "observer/object-relative"

motion, and were, thus, suggested to be driven by the cues resulting from the relative motion between the object and its background. For one of these cells this hypothesis was supported by the results from tests carried out in a darkened room by moving an illuminated object in the cell's preferred direction (see Fig. 9.7). If the cell was driven by the object-relative motion cues, it should not have responded at all in the darkness as the relative motion cues were totally eliminated. The results from the experiments confirmed this. The elimination of the relative motion cues abolished the responses to object-motion in the cell's preferred direction.

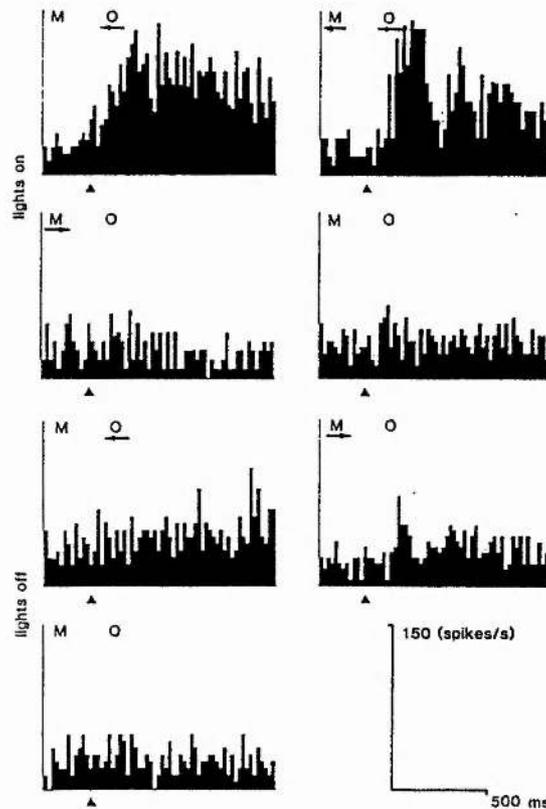


Figure 9.7. A cell (J104_28.50) tested for responsivity in various motion conditions in light (four upper panels) and in darkness (three lower panels). The cell exhibited strong responses to the sight of an approaching object (O). The cell also responded comparably when both the monkey (M) and the object were moved together so that the distance between the monkey and the object remained constant but there was a relative movement between the object and its background ($p > 0.4$). Both of these conditions elicited significantly stronger responses than the stationary object presentation ($p < 0.003$) whereas the cell did not respond above spontaneous activity when the monkey was moved towards the object ($p > 0.8$). The activity during static stimulus presentation is pictured in the fourth panel. (ANOVA, $F_{3,25} = 9.9$, $p < 0.0005$, $n = 6, 8, 6, 9$). In the darkness, the cell failed to respond to an illuminated object movement (or self movement) confirming that the cell responses were driven by relative movement between the object and its background. (ANOVA, $F_{2,24} = 2.2$, $p > 0.1$, $n = 9, 10, 8$). The PSTHs present averaged cell activity collected from five trials (Bin width = 20 ms).

That the lack of responsivity in the "object-relative" condition which was tested with conjoint object- and self-motion reflected *merely* the response discrimination between object-motion and self-motion as described in the previous section, was unlikely for two reasons. First, two of the three cells which responded comparably in the object- and self-motion conditions were also tested in the "object-relative only" condition and still both of these failed to respond in the "object-relative" stimulus condition. Secondly, those three cells which responded in the "object-relative" condition still showed the response discrimination between object-motion and self-motion conditions.

One cell responding preferentially to approaching object motion was also tested with a projected video film where the object and its background were moving independently (see Fig. 9.8). In the video testing the responses were found to be graded depending on the visual motion cues present. Two conditions were found to be incapable in evoking responses above the cell's spontaneous activity; a contracting object against a static background (which provides both observer-relative and object-relative cues about a *retracting* object) and a static object against a contracting background. The latter condition provided object-relative cues about a looming object, but the observer-relative cue implied a static object. It is possible that the contracting whole-field effect may have overridden the effect of object-relative approach thus resulting in no response. This hypothesis was actually supported by the results from the next condition where the object was static but the background was expanding. So, even though this condition provided object-relative cues about a retracting object, the expanding whole-field overrode this effect and resulted in marginally stronger response above the cell's spontaneous activity. The two last conditions resulted in clear responses. In the first of these, an expanding background alone provided at least observer-relative cues about an approaching large object, and it could be argued that this condition included also object-relative cues as the

projecting screen and its immediate surroundings in our experimental situation. A video image of an expanding object against a static background resulted in comparably strong responses.

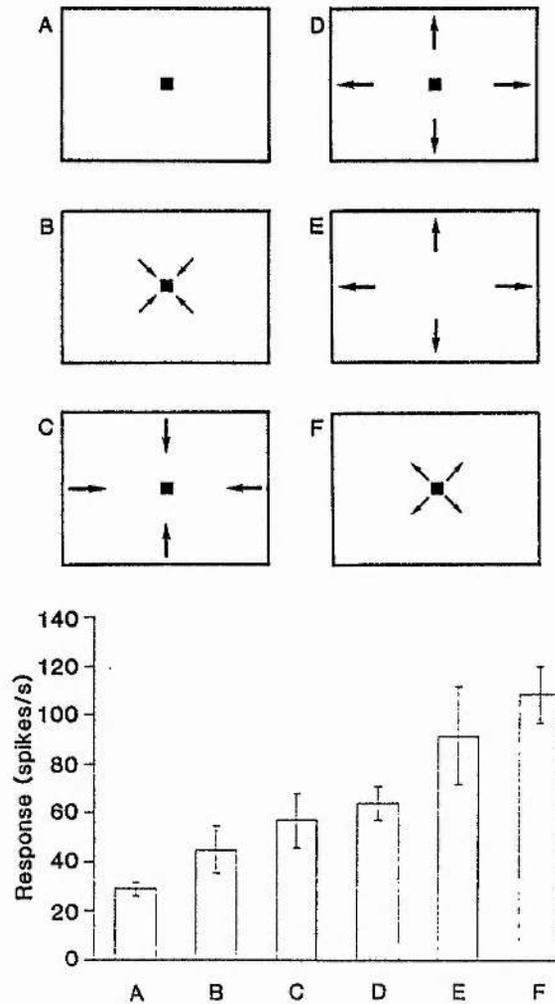


Figure 9.8. Mean responses (± 1 SE) of one cell (J26_26.43) to different video image displays providing observer-relative and object-relative motion-cues. The cell responded preferentially to approaching movement and the responses were graded depending on the visual motion cues present (see text for details). A contracting object against a static background (B) and a static object against a contracting background (C) did not succeed in eliciting responses above the responses to static stimulus display (A) ($p > 0.1$). A static object against an expanding background (D) resulted in marginally stronger response ($p < 0.05$) above the responses to static image. An expanding background (E) and an expanding object against a static background (F) resulted in strong responses above the cell's spontaneous level of activity ($p < 0.001$). (ANOVA, $F_{5,24} = 6.5$, $p < 0.001$, $n = 5$ in each condition).

9.3.4. Eye movements during object-motion and self-motion

For half of the 16 cells that discriminated between object-motion and self-motion the preferred direction of object-motion was either straight towards or away from the animal. As these particular stimulus conditions were unlikely to elicit any systematic eye movements (other than convergent and divergent eye movements), it is difficult to argue for that the response discrimination would have resulted from differential eye movements.

When the testing involved lateral directions of movement (left/right) it is possible that the animal could have been tracking the object during object-motion but not when the animal itself was moved. This would have resulted in dissimilar eye movements in these conditions. The eye movement recordings revealed, however, that the monkey did not execute systematic pursuit movements on every trial during object-motion nor was it always fixating the object while itself moving. Figure 9.9 shows an example of the animal's horizontal eye movements during object-motion to the right and self-motion to the left. Even though there was great variation in the eye movements in both stimulus conditions, no obvious systematic difference was present, yet the cell responded only during object-motion. Interestingly, the eye movement pattern during stationary stimulus presentation resembled closely that during object-motion - but, again, as the rasterograms show, there was a clear response on every trial during object-motion but never during static stimulus presentation. For all of the cells recorded an inspection of the eye movements and cell responses never suggested that the cell responses were linked with the occurrence of saccades, smooth pursuit movements or fixation onsets.

9.3.5. Location of cells

Histological reconstruction in monkeys B, F, D and J indicated that 17 of the 19 tested cells were located in the cortex of the dorsal bank of the superior temporal sulcus.

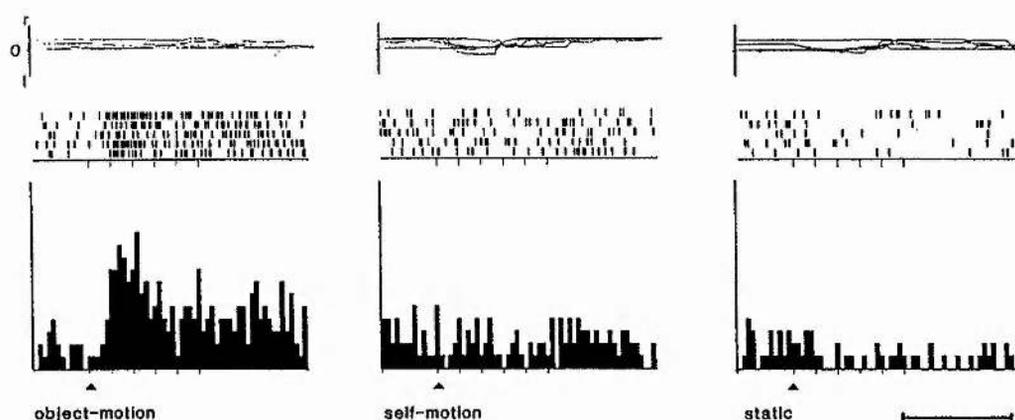


Figure 9.9. Horizontal eye position and discriminative cell responses to object-motion. The cell (J73_33.20) responses to object-motion to the right were significantly stronger than visual responses when the object was stationary and the monkey was moved to the left ($p < 0.0005$). The cell activity during visual self-motion did not differ from that during static stimulus presentation ($p > 0.1$) (ANOVA, $F_{2,12} = 43.2$, $p < 0.0005$, $n = 5$ in each condition). The eye movement recordings show considerable variation within each stimulus condition types, but no systematic difference in the fixation pattern between object-motion, self-motion or static stimulus presentation. The ordinate axes of the PSTHs scale the cell responsivity for 150 spikes/s. The ordinate axis in the eye position recordings give a scale for ± 30 degrees. Time scale (500 ms) shown at the bottom. Small arrow heads below the time axes denote the stimulus onset.

(areas TPO and PGa of Seltzer & Pandya, 1978). 14 out of these 17 cells (82%) exhibited selective responses to object-motion. Three cells which gave indiscriminate responses to self- and externally-induced pattern motion were also located within this same area.

Even though the recordings were aimed at the dorsal bank of the STS, histological reconstruction indicated that 2 of the studied cells were in the ventral bank of the STS (area TEa of Seltzer & Pandya, 1978). Both of these cells also discriminated between object-motion and visual self-motion. Figure 9.10 shows the results of the histological reconstruction in monkey (J) from which the majority of the cells were recorded (14/19).

1986; Tanaka & Saito, 1989; Sugita et al., 1990; Roy & Wurtz, 1990; Duffy & Wurtz, 1991a,b; Sugita & Tanaka, 1991). Based on the observed response properties of single cells in these areas a functional differentiation has been suggested for these areas. Area MT and the ventral part of area MST (MSTv) have been proposed to analyse object-motion characteristics from the retinal image, whereas the dorsal part of area MST (MSTd) has been seen particularly suitable in analysing visual consequences of the animal's own locomotor activity (Saito et al., 1986; Tanaka et al., 1986; Tanaka & Saito, 1989; Roy & Wurtz, 1990; Saito, 1992).

These ideas stem from the observations that some neurons in area MT have relatively small excitatory receptive fields which are surrounded by an inhibitory field. For some cells a particularly effective stimulus is a local movement in the preferred direction restricted within the cell's excitatory field which is surrounded by a large field movement in the opposite direction (null direction). This arrangement produces facilitated responses as compared to those achieved during central area motion against a stationary surround. Despite this, a stationary slit at the center of the excitatory field while the surrounding moves in null direction does not activate the MT cells (Tanaka et al., 1986; Saito, 1992).

The MSTv cells resemble MT cells in that the cells prefer the movements of a bar to whole-field movements but they have larger excitatory fields and the responses are exhibited, for example, to a bar movement anywhere within the excitatory field. Simultaneous *background* movement in the same direction suppresses the excitatory response to the bar movement. It seems, thus, that the effective area for the inhibition and excitation may coincide. This type of inhibition is better described as "background inhibition" to differentiate it from the surround inhibition found in MT cells (Tanaka et al., 1986). However, unlike in MT cells, the relative motion cues alone have been shown to elicit responses in MSTv cells, and furthermore, cells

responding to relative-motion were driven by occlusion-related cues, i.e. appearance and disappearance of the background components (Sugita & Tanaka, 1991).

It seems thus that the MT cells are sensitive to both "observer-relative" and "object-relative" motion cues but in a conditional way so that the cells are not driven by the "object-relative" motion cues alone. Tanaka et al. (1986) concluded that the responses are primarily determined by the vector of the center area movement, but that the response is scaled according to the difference between center and surround movements. This conclusion was also supported by the results from experiments where the background was moved faster than the center area in the cell's preferred direction. Perceptually this condition produces an illusory perception of movement in the center area in the opposite direction to the veridical movement occurring locally on the retina. The cell responses, however, were never observed to reverse their directional selectivity in this condition. The strength of modulation by the surround movement to excitatory central area movement responses was found to vary continuously among MT neurons. The cells in area MSTv, on the other hand, also respond to object-relative motion cues alone. It has been suggested that the surround inhibition observed in MT cell responses could be based on inhibitory feedback projections from area MSTd cells. This area contains a unique type of cells that has large excitatory receptive fields, much larger than those in MT and MSTv, which prefer whole-field movement to small localized object-motion (Tanaka et al., 1986).

Visual neurons in the posterior parietal cortex (area 7a) have also been described responding to relative-motion (Sakata et al., 1985). This is another area in the motion processing pathway which, like area MSTv, receives direct projections from area MT (Maunsell & Van Essen, 1983b; Baizer et al., 1991). Sakata et al. (1985) have reported directionally selective visual tracking neurons which also respond to visual motion when the animal is fixating. They studied the motion responses of these cells by having the animal fixating a stationary spot that was

surrounded by a luminous frame. For some of the cells the preferred direction of the frame movement was the same as that of tracking and they termed these cells "isodirectional" visual tracking neurons. However, half of the neurons preferred the opposite directions for the frame movement and for the visual tracking and were called "antidirectional" visual tracking neurons. Now, the visual motion responses of these "antidirectional" cells seem to reflect object-relative motion coding.

The present experiments showed that some of the STP cells seem to be coding specifically object-relative motion. Three cells, out of the 13 tested for observer/object-relative and object-relative motion, exhibited responses to the relative motion between the object and its background. It is believed that these responses really reflected object-relative coding in area STP and were not just artefacts produced by the experimental set-up. One could argue that the parallel movement between the monkey and the object was not well enough controlled and that some relative movement occurred between these two. This argument, however, does not rest on firm grounds for two reasons. First, as it was explained in the Methods, the experimenter himself served as an "object" for the testing of these motion cells, and it was very easy for the experimenter to have a firm grip from the trolley upon which the primate chair was resting and move it with him. It is therefore unlikely that any substantial relative movement existed between the monkey and the experimenter. Second, the majority of the cells (10/13) failed to respond in this condition and there was no reason to believe that the experimenter's control over the trolley movements would have been less accurate with the other three cells. Finally, and most convincingly, one of the three cells was also tested in a darkened room by moving an illuminated object in the cell's preferred direction and the cell did not respond to this absolute motion lacking the visual cues about object-relative motion.

It is tempting to speculate on the relation of the present results to the questions of how the brain computes a representation of the visual space and directions of

movement in it and what kinds of representations there are coded at different levels of visual areas. The first level of directional representation takes place relative to the retina itself. At the next stage, the visual system must be able to detect object-motion also when there is no retinal movement present, i.e. when an moving object of interest is tracked with slow pursuit eye movements. This results in an "orbitocentric" representation for motion. Evidence for orbitocentric motion representation has been provided by response properties of single units in posterior parietal cortex (Hyvärinen & Poranen, 1974; Mountcastle et al., 1975; Sakata et al., 1985) and in areas MT and MST (Komatsu & Wurtz, 1988a,b; Newsome et al., 1988) which respond preferentially during smooth pursuit of small moving targets. At the next level of space and motion representation, i.e. in the egocentric frame of reference, the location of objects and direction of motion are related with reference to the "self". This requires that not only eye movements, but also head movements and movements of the limbs are encoded together with motion (or location) of objects in the external world. The posterior parietal cortex has been repeatedly connected with the analysis of the relationship between objects in the space and the self (Lynch, 1980; Hyvärinen, 1982).

It would seem that area STP also analyses visual motion in an ego-centered frame of reference. Even though the present studies do not provide any unequivocal evidence for this hypothesis, two following observations seem to point strongly in that direction. First, the animal's eye movements did not affect the directionally selective motion responses in STP units. This property requires that the direction of object-motion is analyzed independent of the direction of movement on the retina or eye position in the orbit, i.e. in an egocentric frame of reference. Second, most of the units (10/13) tested for observer-relative and object-relative motion cues failed completely in responding to object-relative motion cues but required a real relative motion to be present between the monkey and the moving stimulus. However, it should be noted that egocentric motion coding could actually take place at the stage before STP, in

area MST. It is known that this area receives direct projection from parietal cortex and this input could be carrying the necessary information for observer-relative motion coding (Boussaoud et al., 1990).

The hypothesis for egocentric coding for movement also receives indirect support from studies showing that in the majority of STP units the recognition of static form (heads) is based on viewer-centered frame of reference (Perrett et al. 1989b, 1991). Furthermore, it has been suggested that the function of these cells could be to code the direction of attention of other animals in social situations, rather than taking part in object recognition (Perrett et al., 1992). Obviously, this type of function would be most efficient when carried out in an egocentric frame of reference. There is also some evidence that area STP may also process motion information using a frame of reference that is different to the egocentric co-ordination system. Perrett et al. (1989c, 1990a) has described STP cell responses reflecting "goal-centered" coding, e.g. movement of an object towards another object in the environment. This type of coding is particularly effective in describing *actions* of other organisms, relating the agent of the action to the goal of the action.

Lack of responsivity to visual cues of self-motion. The main result of the present experiment was that the motion sensitive cells in area STP do not respond to visual motion stimulation which results from the animal's own locomotor movement. This is the first experiment to study visual responsiveness in cortical motion processing areas to stimulus motion which results from *actual* movements of the animal. Neurophysiological studies from the visual motion areas preceding area STP, namely areas MT and MST, have suggested different functions for these two areas in detecting object-motion and self-motion, respectively, but the studies have often been carried out in anaesthetized animals and only with stimulation mimicking visual consequences of self-motion. Furthermore, while MST may function in processing whole-field visual flow patterns during locomotion, i.e. *detecting self-motion*, area

STP would appear to have complementary functions in *detecting object-motion* as the neurons in STP did not respond during self-motion.

The results suggest that area STP differentiates between visual motion that results from movements of external (animate or inanimate) objects and movements of self. One of the several functions proposed for visual motion sensitivity is that it provides an estimate of the "time to collision" (see Nakayama, 1985). It seems that the processing of visual flow patterns which provide estimates of "collision" may be innate and, furthermore, innately associated with triggering compensatory reflexes. Bower et al. (1970) and Ball and Tronick (1971) have reported that young babies without experience about the effects of colliding objects exhibit defensive distress reactions (pulling the head backwards and raising arms to cover the face) to "looming" display images. Similar results have been reported with infant rhesus monkeys (Schiff et al., 1962). It is obvious, that the visual system must be able to separate instances when the flow results from animal's own movements and when there is no need to trigger defensive or orienting reflexes.

Grüsser and Landis (1991, pp. 372-379) have recently described their observations with a patient (L.M.) suffering from akinetopsia (visual movement agnosia) following from bilateral brain lesions in the occipito-temporal region. The patient's symptoms were originally studied and described by Zihl et al. (1983) and were characterized by her difficulties in discriminating between moving and stationary objects or estimating their speed and direction. Now, Grüsser and Landis (1991) provide a following observation which is of particular interest in here: "when walking across the garden or along the street, she reported that she had the impression that the objects in her extra-personal space were moving up and down." Grüsser and Landis concluded that "this apparent motion was evidently related to her own body movements while walking." In a follow up study Zihl et al. (1991) concluded that the patient's impairment in perceiving visual movement was caused by lesions of a brain

region that includes an area corresponding to area MT in primates. It is fascinating to speculate that the patient's lesions might have extended to cover or disconnect a brain region which corresponds area STP in monkeys. The results described in the present study make it very tempting to suggest that STP lesions might produce exactly the disturbances manifested by L.M.: difficulties in discriminating between visual image motion originating from external sources and motion resulting from one's own locomotor activity.

Another benefit of suppressing responses to visual self-motion may be that this way the visual system enhances its capacity to detect object-motion relative to the objectively stationary environment in the situation where the perceiving subject is moving itself in the environment. Psychophysical experiments with humans have shown that thresholds for the detection of external object motion are elevated under conditions which mimic the visual whole-field flow stimulation received during natural locomotion (Probst et al., 1986). The patient L.M. discussed above had also particularly severe difficulties in discriminating static from moving objects when she was moving (Grüsser & Landis, 1991). The present experiments were not designed to make any inferences about object-motion detection during self-motion, but interestingly the results showed that the responsivity of 2 cells (of the nine cells tested) to object-motion was attenuated during self-motion.

The interesting question is what kind of information is used for the observed response discrimination between object-motion and self-motion? The results showed that the majority of the tested cells which discriminated between object-motion and self-motion were classified as responding to "observer-relative" motion cues. This conclusion was drawn from the results showing that the cells responded to object motion in the light (includes both observer- and object-relative cues) but failed to respond when the observer-relative cues were eliminated by moving the object together with the monkey in the same direction. Now, admittedly the object-relative

cues differed slightly in these two testing situations. This difference, however, should not have produced any significant effect on the cell responses as the responses were found to be very tolerant for the variation in stimulus speed within a range that well exceeded the differences present in object-relative velocity fields between the two testing conditions (see below).

The "observer-relative" motion cues do not differ between object-motion and self-motion conditions and this fact gives support for the hypothesis that the response discrimination in STP must be in part based on extraretinal factors. Most convincingly, the cell which was depicted in Fig. 9.6 showing "observer-relative" responses to object-motion in the dark, showed also response discrimination between object-motion and self-motion, in a condition where retinal factors could not possibly contribute to the response discrimination.

Three cells were shown to be driven by object-relative motion cues which suggests that the response discrimination in these cells might have been based on the discriminative retinal changes following from object- and self-motion. A closer inspection reveals, however, that this is impossible. The retinal object-relative motion information that theoretically could be used for providing discriminative responses to object-motion and self-motion is the local velocity at which the object covers (or uncovers) its background. For example, even if object-motion and self-motion had identical speed, the local velocity field on the retina would be different in these two image-motion situations. This results from the differential distance between the observer and the object in relation to the visual background. So, in order to use local velocity cues for response discrimination between object-motion and self-motion the cells should be very narrowly tuned for local velocity field discrepancies. This would mean, however, that the cell would not detect object-motion either when the object is moving even at a slightly different speed from the cell's "optimal" velocity. In the present experiments, however, all the cells were found responsive over a range of

object-motion velocities and despite the inherent variation in the stimulus speed the cells responded consistently only to the object-motion. In summary, there are good reasons to believe that the response discrimination between object-motion and self-motion in STP is not based on retinal factors. Not even with the cells which were suggested to be driven by the retinal cues.

So far self-motion has been discussed only in the context of visual consequences of the observer's locomotor actions. Under natural, environmental conditions the visual system, however, does not work in isolation, but interacts with other sensory systems active during self-motion. This is evident from numerous experiments showing that visually induced perception of "illusory" self-motion (a sensation of subjective motion in an objectively stationary subject) can be modulated by simultaneous vestibular or somatosensory stimulation (Brandt et al., 1973, 1977; Dichgans et al., 1978; Berthoz, 1981; Bles, 1981; Probst et al., 1985; Hlavacka et al., 1992).

Neurophysiological single-unit studies have shown that self-motion signals from different sensory systems combine at the subcortical level in vestibular nuclei (Waespe & Henn, 1977) and in thalamus (Büttner & Henn, 1976; Büttner & Lang, 1979). At the cortical level the vestibular system has been shown to project to several areas: area 2v in the anterior parts of the intraparietal sulcus (Schwartz & Fredrickson, 1971; Büttner & Buettner, 1978; Büttner & Lang, 1979), areas 7a and 7b in the posterior parietal cortex (Pause & Schreiter, 1980, Kawano et al., 1984), and area PIVC (parieto-insular vestibular cortex) in the upper bank of the lateral sulcus (Grüsser et al., 1990a,b). Thier and Erickson (1992) have also shown that cells in the lateral part of area MST (MSTl) do receive a head-movement related non-visual input which probably originates from the vestibular organs. These studies have been investigating the cell responses during "pure" vestibular stimulation (body rotation in darkness), during optokinetic whole-field stimulation (which leads to an illusory

sensation of self-movement) and during combined vestibulo-visual stimulation. Interestingly, none of the recorded brain areas have revealed cells responding to "pure" optokinetic stimulation but not to the same visual motion when it results from self-motion.

Area STP has been shown to receive direct projections from areas 7a and 7b (Pandya & Kuypers, 1969; Jones & Powell, 1970; Selzer & Pandya, 1978, 1984; Morel & Bullier, 1990). It is well documented that, in addition of exhibiting unimodal visual, auditory and somatosensory response characteristics, the activity of some single neurons in this area can be modulated by input through more than just one sensory modality (Bruce et al., 1981; Benevento et al., 1977; Mistlin & Perrett, 1990). The results from the experiments described in the two previous chapters also suggested strongly that motor/somatosensory input was used to inhibit responses to visual stimulation that resulted from the monkey's own actions (the sight of its own arm movements and self-generated pattern movement). In the present experiments the possibility of motor input influencing cell responses can be ruled out quite confidently, whereas the vestibular-visual and/or somatosensory-visual interactions seem a strong candidate in providing a physiological mechanism for the response discrimination in visual responses between object-motion and self-motion. It should be remembered that in natural conditions when the animal is actively walking, motor (corollary discharge) signals are likely to have an additional influence on this discriminative neural capacity.

The present experiments do not allow very detailed models to be made of the nature of the neuronal mechanisms mediating the observed response discrimination. A simple vestibular/somatosensory inhibition acting directly on the recorded STP units can, however, be ruled out unequivocally. This is evident from the results which showed that the cells continued responding to external object-motion in spite of the concomitant self-motion, providing that relative movement between the monkey and

the object was present. One possible mechanism would be that the "self-motion" input is used to subtract the visual consequences of monkey's own movement from the "total" motion input. This type of mechanism would impose very demanding requirements for the data transformations in translating the visual and the vestibular/somatosensory signals into a compatible format for carrying out the subtractive computations. This type of computational problem has also been raised in the context of visual stabilization during eye movements and MacKay (1973) has proposed a model which is modifiable to provide a framework in interpreting the present results as well. According to the model the sensory changes due to self movements do not need to be eliminated from the sensory input, but to be appropriately evaluated. Perceivers build up an internal representation ("a map") from their environment which is stored and expected to be invariable. Changes in sensory input caused by self movements would not contribute to any information of the environment itself and should not modify the representation. The function of the "self-motion" signal would, therefore, be to provide information (or set criteria) to the central mechanisms as to whether incoming afferent sensory signals require a readjustment of the internal representation of the environment.

In conclusion, the present experiments suggest that the direction of motion is predominantly represented in an egocentric frame of reference in area STP and that one of the major functions of this area in motion processing is to detect object-motion. This requires discrimination of the visual consequences of external object motion and the image motion resulting from the animal's own body movements. These results provide further evidence for area STP's role in processing preferentially "unexpected" stimulation and ignoring "expected" sensory consequences which result from one's own actions.

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