

SOCIAL SIGNALS ANALYZED AT THE SINGLE CELL LEVEL: SOMEONE IS LOOKING AT ME, SOMETHING TOUCHED ME, SOMETHING MOVED!

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ABSTRACT: In the superior temporal sulcus (STS) of the macaque brain there are populations of cells which respond selectively to faces. Studies of these cells reveal that they are very sensitive to the direction of eye gaze and posture of the head of other subjects. It is argued that one function of the cells is to enable analysis of where other individuals are directing their attention. Given this selectivity for complex socially relevant stimuli it is surprising that the STS contains cells that respond to touch anywhere on the body or to any movement seen in the visual environment. We have investigated these tactile and motion sensitive cells to determine their behavioural significance. In the awake, behaving monkey we found that the critical dimension for polymodal coding is whether or not the sensations are expected. Tactile stimulation out of sight cannot be predicted and elicits neuronal responses. By contrast, when the monkey can see and, therefore, predict impending contact, or when the monkey touches a familiar surface in a predictable location, cell responses are reduced or abolished. In an analogous way some cells are unresponsive to the sight of the monkey's own limbs moving but respond to the sight of other moving stimuli. Since unpredictable sensations are often caused by other animals, the STS area appears well suited to defining sensory stimuli that are important in social or predator/prey interactions.

INTRODUCTION

We have been studying the properties of single neurons in one region of the association cortex of the macaque monkey. Figure 1A illustrates a side view of the brain with the site of study indicated with cross hatching. Visual information arrives in the cortex at the back of the brain and has been processed in several prestriate regions before reaching the study site within the superior temporal sulcus (STS) (Jones & Powell, 1970; Seltzer & Pandya, 1978). The STS also receives anatomical input from the parietal association cortex, an

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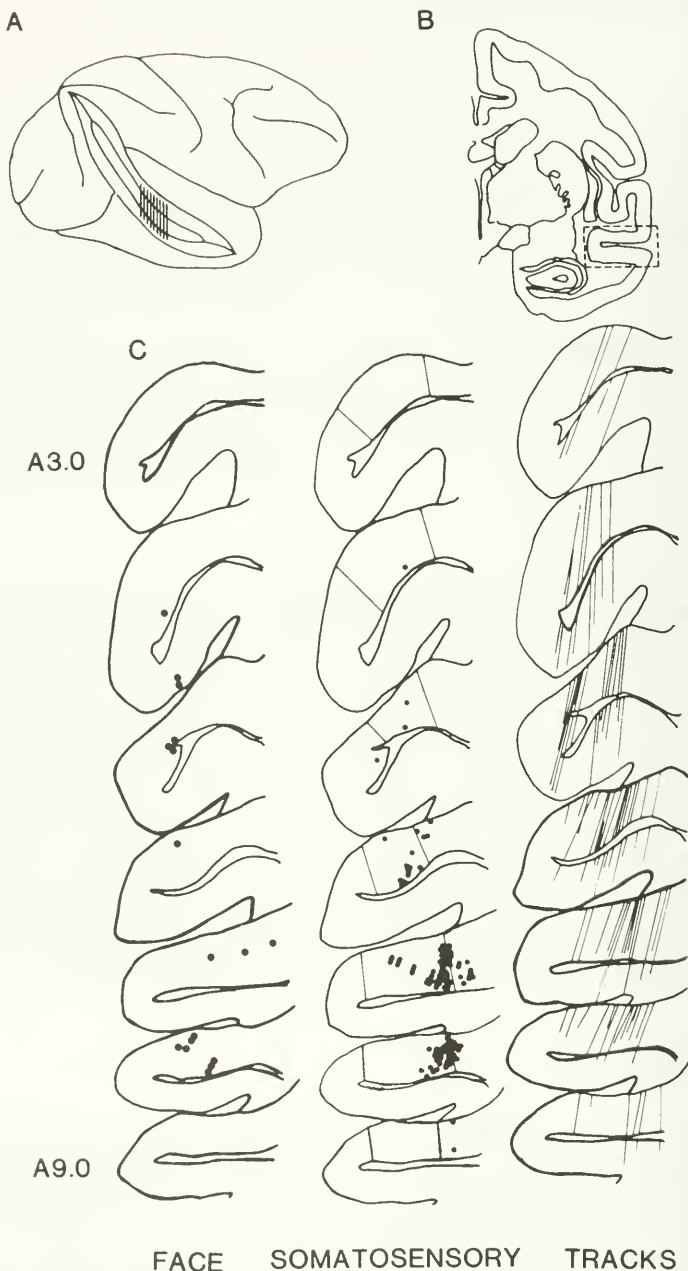


FIGURE 1. Histological location of study site. (A) A schematic drawing of a sagittal view of a rhesus macaque brain showing the position of recordings (cross-hatching) within the opened superior temporal sulcus (STS). (B) A coronal section of the right hemisphere with a box around the STS. (C) Serial coronal sections illustrating the distribution of cells selectively responsive to faces (left) and somatosensory stimulation (middle) and the location of electrode trajectories (right).

area involved in processing tactile and visual information and in motor control (Hyvärinen & Poranen, 1974; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Lynch, Mountcastle, Talbot, & Yin, 1977; Leinonen, Hyvärinen, Nyman, & Linnankoski, 1979; Seltzer & Pandya, 1984). The STS projects to a variety of brain systems but has particularly strong connections with the amygdala, a system implicated in the control of social and emotional behaviour (Aggleton, Burton, & Passingham, 1980).

The STS is involved in processing a variety of information in visual, auditory, and somatosensory modalities (Bruce, Desimone, & Gross, 1981). For the visual modality a number of studies have reported cells selectively responsive to complex stimuli such as hands and faces (Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Rolls, 1984; Baylis, Rolls, & Leonard, 1985). Given the selectivity of cells for faces and the connections with the amygdala, it is argued that the STS might function to provide an analysis of stimuli relevant to social interactions.

In the first half of the paper it will be argued that one of the main functions of the analysis is to provide cues to where other individuals are directing their attention. This functional role has been largely overlooked in studies describing sensitivity to different perspective views of the head (Bruce et al., 1981; Desimone, Albright, Gross, & Bruce, 1984; Perrett et al., 1982; 1985a; Perrett, Mistlin, & Chitty, 1987; Perrett, Mistlin, & Harries, 1989a; Perrett, Harries, Mistlin, & Chitty, 1989b; Perrett et al., 1989c; Hasselmo, Rolls, Baylis, & Nalwa, 1989).

The function of sensory information processing in other modalities in the STS has been less obvious since much of the processing seems to lack selectivity (Bruce et al., 1981; Hikosaka, Iwai, Saito, & Tanaka, 1989). Consideration of the difference between sensations arising from the monkey's own movements and social interactions involving the actions of other individuals, however, reveals that STS processing of somatosensory information is also highly selective (Chitty, Mistlin, & Perrett, 1985; Mistlin, Perrett, & Chitty, 1986; Mistlin & Perrett, 1990; Perrett, Mistlin, Harries, & Chitty, 1989d).

The second part of the paper is devoted to a consideration of the processing of somatosensory information and visual motion in the STS. Cells in the STS appear to be selectively responsive to sensory events arising from other individuals and are able to ignore the equivalent but predictable sensations that are self-produced.

The capacity to ignore predictable self-produced sensory input has received little consideration except for research on the stabilization of the visual world independent of eye movements (Wallace, 1985; Galletti, Battaglini, & Aicardi, 1988). Despite this, the discrimination between self-produced and nonself-produced events is proba-

bly fundamental to information analysis in sensory systems throughout the animal world (Sperry, 1950; von Holst & Mittelstaedt, 1950; Bell, 1989). The sensitivity of STS cells to unexpected stimulation allows them to be preferentially activated by stimuli arising from other individuals. This capacity could allow them to play an important role in detecting predators and in social interactions with other monkeys.

I. SENSITIVITY TO HEAD POSTURE AND TO GAZE DIRECTION

Recordings from the STS have revealed populations of cells that respond selectively to faces and other views of the head (Perrett et al., 1982, 1985a). The first part of the paper reviews studies of cells responsive to the head that we have made over the last 10 years. We describe a theoretical re-evaluation of cell function and recent developments in our analysis of how information relevant to social interaction (posture and gaze) affects discharges in these cells. Head posture and direction of gaze are signals which play an important role not only in human society (Argyle & Cook, 1975) but also in nonhuman primate societies (Perrett & Mistlin, 1990). For example lowering of the head and direct eye contact for monkeys are components of threat gestures (Bertrand, 1969; Hinde & Rowell, 1962; van Hoof, 1967). The act of averting the head and gaze may act as a submissive signal (Chance, 1962; Redican, 1975; Perrett & Mistlin, 1990).

GENERAL METHODS

We recorded the activity of single cells in awake behaving monkeys (5 *Macaca mulatta* and 2 *Macaca arctoides*). From 500 to 1,500 cells were studied in the temporal cortex of left and right cerebral hemispheres of each monkey. Details of recording techniques are given in brief here (for details see, Perrett et al., 1985a, 1985b). Before recording work began, the experimental animals were trained to sit in a primate chair and to perform visual discrimination tasks, giving a lick response for a fruit juice reward. This ensured that they attended to visual stimuli presented. When trained, a 15 mm stainless steel ring (recording chamber) was attached to the skull under barbiturate anaesthesia and full sterile surgical procedures. One month later, recordings began and were made 2-3 times a week for approximately 1 year. During each recording session (1-4 hours) the animal was seated in the primate chair. A miniature hydraulic microdrive was attached to the stainless steel recording chamber and a small microelectrode (insulated tungsten wire with an uninsulated

tip 10 microns diameter, 10-15 microns long) was advanced into the cortex of the temporal lobe. Between recording sessions the micro-electrode was removed and the monkey was returned to its home cage.

The electrical activity from the brain recorded through the micro-electrode was amplified and signals outside the relevant band (0.5-20 kHz) filtered. Brain activity was visually displayed on oscilloscopes and action potentials from an individual cell selected on the basis of voltage amplitude and duration. These were arranged to trigger digital pulses which were then analysed by computer. Real or photographic visual stimuli were presented from behind an electromagnetic shutter (Compur, 6.4 cm aperture). Each cell was tested with a range of different views of the head and body, and a range of different directions of motion. Where cells were found responsive a variety of other control stimuli were studied. The responses of individual neurons to 3-D or 2-D stimuli were measured during the period 100-350 ms after the presentation of a stimulus. This period was chosen because the majority of cells in the temporal cortex responded with latencies of 100-150 ms. The position of cells recorded in each hemisphere was reconstructed from histology and frontal and lateral xrays taken at the end of each recording track (e.g., Figure 1).

RESULTS

Different populations of cells in the temporal cortex responded to different types of stimuli. For different experimental subjects, 40 to 60% of cells remained unresponsive during testing and were unclassified. Of the classified cells, on average 46% responded to static visual stimuli; 10% selectively to the sight of the head or body; 4% to objects other than bodies and 32% without apparent form selectivity. Thirty-eight percent of the classified cells were motion sensitive; 11% responding selectively to body motion; 2% responding to objects other than bodies moving and 25% responded to particular types of motion without form selectivity (Perrett et al., 1985b, 1989d; Perrett, Harries, Benson, Chitty, & Mistlin, 1990a; Perrett, Harries, Chitty, & Mistlin, 1990b). Sixteen percent of the classified cells responded to tactile or auditory but not visual stimuli.

This section deals only with those responsive to different views of the head. The proportion of cells in the upper bank of the STS that were found selectively responsive to the face and head varied from study to study, ranging from 1-20% (average 10%). This variation probably reflects a modular or clumped organization of cortex, and possible asymmetry in hemispheric distribution (Perrett et al., 1988). Within a clump extending 3-4.0 mm across the temporal cortex cells

have a higher probability of responding to the same type of stimulation than outside the clump (Perrett et al., 1984, 1985a, 1985b, 1987).

In an early study of 182 cells selectively responsive to the sight of the head, 63% were found to be sensitive to perspective view of the head (Perrett et al., 1985a). Discrete populations of cells were found to be maximally activated by different views of the head. In the horizontal plane separate populations were found to be selective for the face, left and right profile, and back of the head views. In the vertical plane, two further types of cell were found to be selective for head raised and head lowered.

THE USE OF CHARACTERISTIC VIEWS FOR RECOGNITION

For several years we assumed that the function of the cells responsive to faces and to other views of the head was to facilitate the recognition of the stimulus as a head (Perrett et al., 1984, 1985a, 1987) or as an individual, since some cells were sensitive to the differences between faces (Perrett et al., 1984, 1989a, 1989b, 1989c; Baylis et al., 1985). We argued that cells were tuned to particular perspective views because the views were visually different. If recognition was to be successful from all views then different views would need to be separately coded. Cells tuned to the face and other views of the head show considerable generalization for the preferred view despite changes in retinal position (Desimone et al., 1984; Bruce et al., 1981; Perrett et al., 1989a), size (Perrett et al., 1982, 1984; Rolls & Baylis, 1987), orientation (Perrett et al., 1984, 1985a) and lighting (Perrett et al., 1984). Cells tuned to one perspective view can therefore be seen as providing a high level description covering almost all instances of that view.

It can be argued that only a limited number of such high level descriptions need to be constructed to cover all the possible ways in which a head can be seen. From the initial studies of view (Perrett et al., 1985a) it appeared that cells were selectively tuned for just four "characteristic" views in the horizontal plane (face, left and right profiles and the back of the head). Although cells were sensitive to change in perspective view tuning for view was fairly broad. For most cells, rotation of the head 60 degrees away from the optimal view reduced the rate of response to only half that of the optimal view (Perrett et al., 1985a; Perrett et al., in press). Thus, populations of cells tuned to the four characteristic views could cover intermediate views such as the half profile. The notion of selective coding of particular characteristic views accords with the results of some psychological experiments and current ideas in mathematical and computational approaches to visual recognition (see Perrett & Harries, 1988, for review).

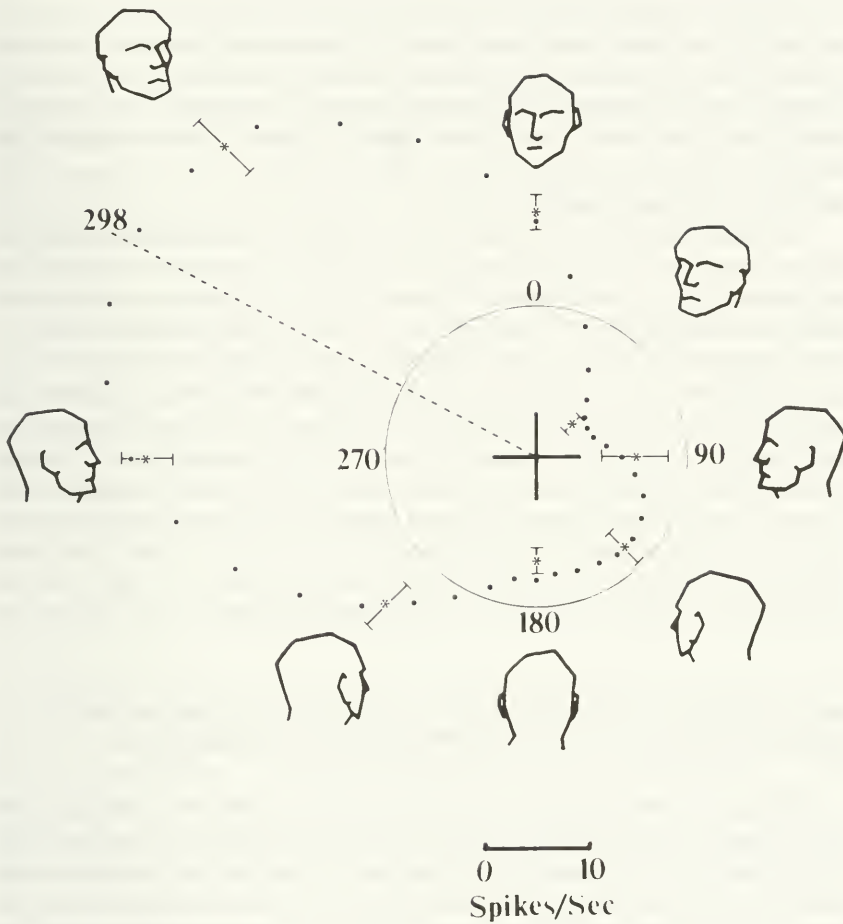


FIGURE 2. Sensitivity to perspective view of the head in the horizontal plane. The magnitude of one cell's response (mean \pm 1 S.E. from 10 trials) to 8 different views of the head is illustrated by the distance from the central cross to the star (bracketed by the error bars). A schematic illustration of the head view at different angles is given around the perimeter. The dotted line provides an interpolation of the cell's tuning curve to different views, it plots the best fit second order cardioid function relating observed response to angle of view. The estimated angle of view producing maximal response is indicated by the dashed line. The central solid circle denotes the level of the cell's spontaneous activity.

Having coded each of the separate views, outputs could be pooled to establish a description of a head or person which holds from all views. This level of coding is comparable to the object centred coding of Marr and Nishihara (1979; Marr, 1982). It should be noted, however, that their model constructs object centred representations directly from surface orientation and does not use an intermediate stage representing specific views.

Results from recent physiological studies confirm the selectivity for perspective view but indicate that cells are tuned to *many* different views. The optimal views for individual cells are not restricted to the four prototypical views (Perrett et al., 1989a; Hasselmo et al., 1989; Perrett et al., in press). Figure 2 illustrates the tuning of one cell to different views of the head in the horizontal plane. This cell is maximally responsive to the half profile view of the head (rotated to the monkey's right by approximately 45°). The preferred view is, thus, directly in between the proposed face and profile characteristic views. From the arguments above it seems then, that more views are coded than are needed to allow recognition from any view. This then presents a puzzle as to *why* so many views are coded. If they are not necessary for object recognition what are they for?

CELLS TUNED FOR DIFFERENT VIEWS OF THE HEAD: A ROLE IN RECOGNIZING FACES OR DIRECTION OF ATTENTION

The cells responsive to the sight of the head may not have one single function. By exploring other possible functions it may be possible to provide an account of why so many views receive separate coding. One account makes the assumption that a cell's function is to detect those stimulus dimensions to which it is maximally sensitive. When a head is observed, the variation in response across the view sensitive cells in the STS could provide collectively an accurate description of the direction in which the head is pointing relative to the observer. Perhaps this then is a function of the cells; to specify the head direction. Such coding could provide an index of where other individuals are directing their attention. A cell maximally responsive to the left profile thus provides a signal that the attention (of another individual) is being directed to the observer's left. Such information is undoubtedly useful for analyzing a great variety of social interactions between other individuals, working out who is threatening whom, who is soliciting support from whom, and whether one's infants or "friends" are being approached, threatened, etc.

One could ask again why so many views need to be coded to specify direction of another's attention. Here the question is misdirected; if one is attempting to recognize a person, then head orientation

(view) is an irrelevance to be overcome, but if one is coding direction of an individual's attention, then the head orientation is useful. The more accurately the STS cells can specify head view, the more accurate the inference about the direction of attention. Thus while recognition needs only a few key views to be selectively coded, the analysis of where someone else is facing (and directing attention) benefits from having a wide range of head views selectively activating different cell populations.

If only four head views (face, left and right profile and back of head) were coded, then recognition of the half profile and other intermediate views would require a comparison between the amount of activation of the populations tuned to the four views. A left half profile would be indicated if face and left profile views were activated to an equal extent and the other two characteristic views were not activated. With a whole range of views explicitly coded (activating different cell types) then further processing is less complicated. View or direction is indicated by the maximally activated cell type.

VERTICAL HEAD ORIENTATION

The ascription of this social function to cells coding head view also makes sense of the tuning observed in many cells to head posture in the vertical plane (Perrett et al., 1985a). Two classes of cells were found to be selective for the head down and the head up. These cells generalized across change of perspective view in the horizontal plane. Cells coding the raised head responded to the face, profile and back of the head views when the head was raised. Similarly cells coding head down generalized across front, side and back views of the head when the head was lowered.

It is difficult to see why generalization should exist only for head up views and not extend to head level views if the cells have a function in recognizing the object as a head from any view. By contrast an account based on directed attention naturally extends to cover the generalization. All views of another individual with head raised indicate a focus of attention directed somewhere above the viewer's head. Similarly all views of the head down imply a focus of attention low in the environment, below the observer.

GAZE DIRECTION

In most cases the direction in which an individual's head is pointing is a good index of where his or her attention lies, but gaze direction is a better guide to focus of attention. This leads to several pre-

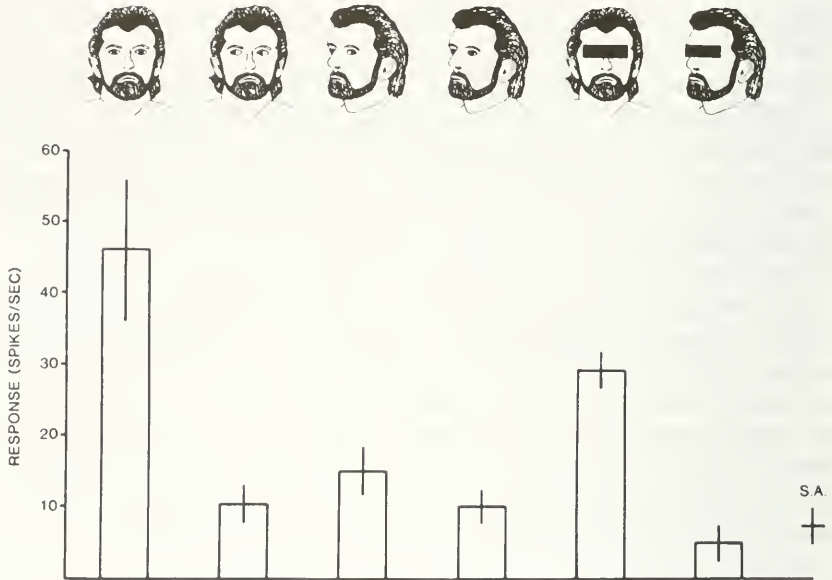


FIGURE 3. Sensitivity to head and eyes directed to the viewer in the horizontal plane. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of the responses of one cell (M047) to the stimuli. S.A. = spontaneous activity. [Number of trials per condition (N) = 6, 5, 4, 4, 3, 4, 6].

dictions for cell tuning to gaze direction: (1) gaze direction should be important to STS cells; (2) when cells are tuned to both head angle and gaze angle the optimal angles for the two cues should coincide and (3) gaze direction should be more important than head view.

These predictions receive some confirmation from previous data. The majority (36 out of 56 tested) of the cells sensitive to head view were also sensitive to gaze direction (Perrett et al., 1985a). For all of these cells the preferred gaze direction was compatible with preferred head direction. That is, cells selective for the face view responded more to eye contact than to laterally averted gaze, while cells selective for the head turned laterally away from the monkey responded more to laterally averted gaze. Of even more relevance was the observation that sensitivity to gaze direction could overwrite sensitivity to head view (see below).

SENSITIVITY TO EYE CONTACT: ATTENTION DIRECTED TO THE VIEWER

Eighteen cells selective for the face view preferred eye contact to averted gaze. This is illustrated in Figures 3, 4 and 5 for cells sensi-

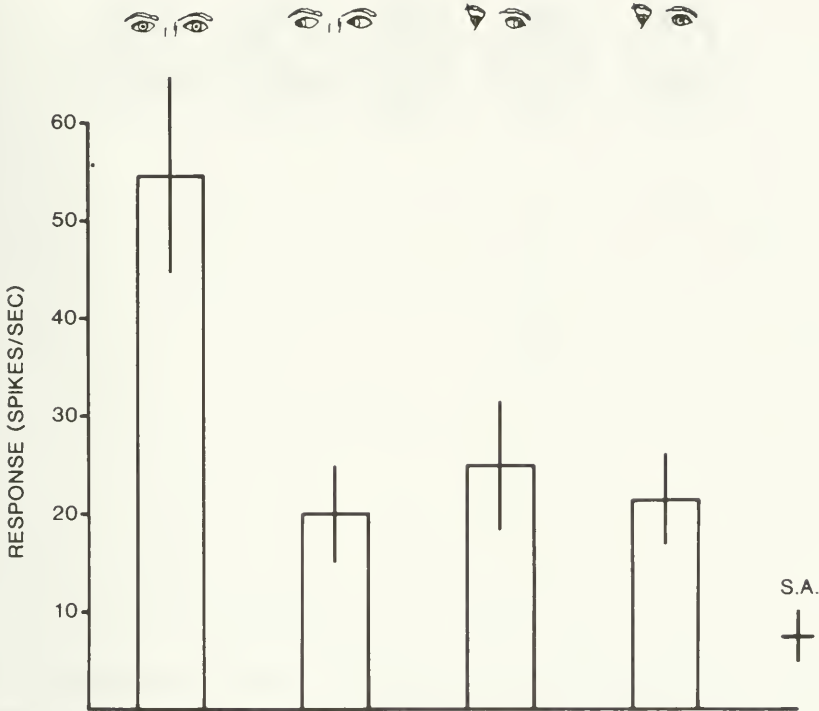


FIGURE 4. Sensitivity to eye contact with the eyes viewed in isolation. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (M047) to restricted views of the eye region. [$N = 6, 6, 5, 4, 5$].

tive to gaze direction in the vertical and the horizontal planes. For the cell illustrated in Figure 3 head view and gaze direction are independently important. With the eyes occluded by a bar the cell showed a preference for the full face view over the half profile view ($p < .05$, Newman-Keuls). Here the eyes are not visible so the discriminative response to head view must be based on other features of the head.

With the eyes visible and gaze aimed in different directions the cell was more responsive to eye contact for the full view than to other views with either the face or eyes averted laterally by 45° ($p < .05$, each comparison). In this instance the cell was selective for eye contact with only the full face view (overall effect of conditions: $F(6,29) = 7.2$, $p < .001$; number of trials per condition (N) = 6, 5, 4, 4, 3, 4, 6). A more common pattern of sensitivity was for cells to display a preference for eye contact for both views of the head (i.e., independent of head position in the horizontal plane). The pattern of eye gaze direction for this cell is replicated in a situation where only the eyes remain visible and the rest of the face is screened from view (Figure

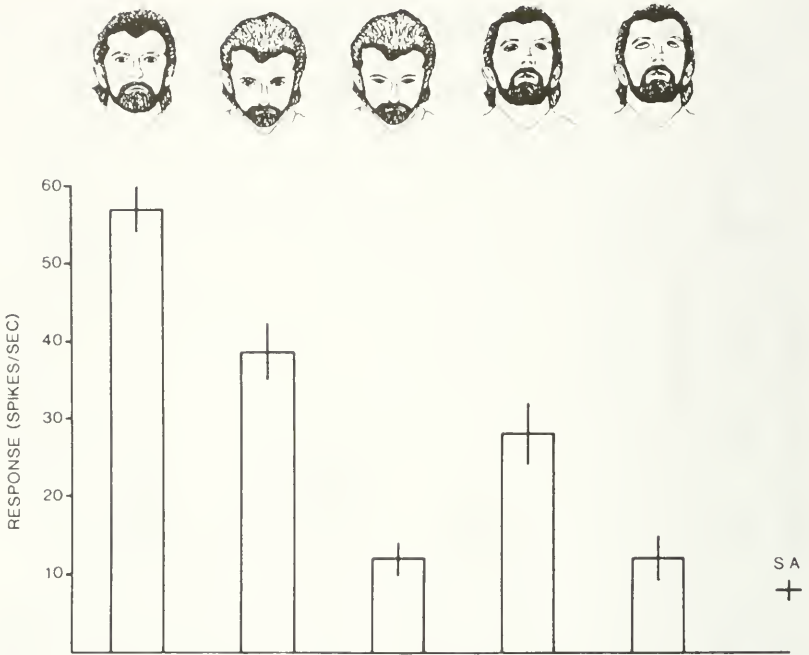


FIGURE 5. Sensitivity to gaze directed to the viewer in the vertical plane. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (P050) to the stimuli. [$N = 5, 3, 7, 3, 6, 7$].

4). The frontal view of the head with eye contact produced a response significantly greater than spontaneous activity and the responses to the face or eyes laterally averted ($p < .02$, each comparison; overall effect of conditions: $F(4,21) = 6.1$, $p < .005$; $N = 6, 6, 5, 4, 5$).

Sensitivity to eye contact was also found for different head views in the vertical plane. This is illustrated in Figure 5 for a cell which responded more to the full face view than to the face rotated 45° up or down ($p < .05$, each comparison). For the head rotated up and down the cell was more responsive to gaze directed to the observer than to the same head views with vertically averted gaze (overall effect of conditions: $F(5,25) = 40.8$, $p < .001$; $N = 5, 3, 7, 3, 6, 7$). For these latter views the eyes are also turned away from the observer. The cell's response to head up and head down was augmented when eye contact was made ($p < .05$, each comparison). The cell is, thus, selective for eye contact independent of the vertical orientation of the head. While the cell may have an overall preference for the full face view it would be erroneous to conclude that the sole function of the cell was to detect

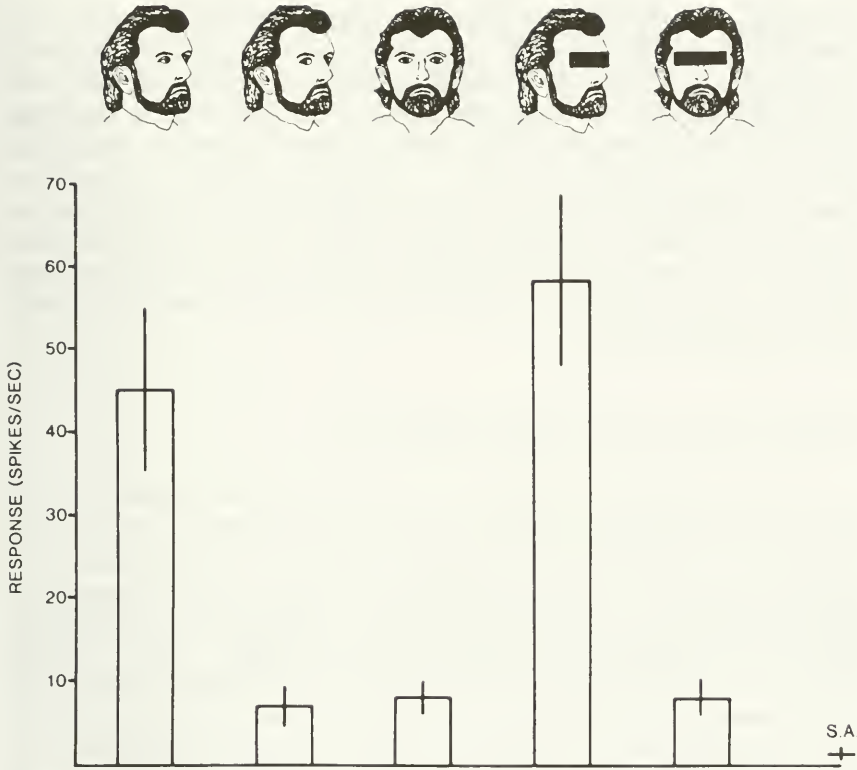


FIGURE 6. Sensitivity to head and gaze directed to the side. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (A086) to the stimuli [$N = 6, 7, 7, 6, 5, 6$].

the face view. The sensitivity to eye gaze is more consistent with a role in specifying attention directed at the observer.

ATTENTION DIRECTED Laterally AWAY FROM THE VIEWER

Many of the cells in the STS are sensitive to the head turned away from the observer in the horizontal plane. For some of these cells the preferred angle of view is one in which the head is turned away to such an extent that the eyes are not visible. For other cells with preferred views closer to the full face it was possible to examine the sensitivity to laterally averted gaze. Eighteen cells selective for the head turned away from the monkey also responded more to laterally averted gaze.

The cell illustrated in Figure 6 responded more to the head

turned 45° away from the monkey than to the full face view ($p < .001$). This difference between head views was also found with the eyes covered ($p < .001$). With the face and eyes visible the cell responded more to the half profile view with laterally averted gaze than to the same head view with eye contact ($p < .001$) (overall effect of conditions: $F(5,31) = 15.4$, $p < .0001$; $N = 6, 7, 7, 6, 5, 6$). Covering up the eyes does not eliminate the response and therefore the cell must be assumed to be sensitive to other regions of the profile. With the half profile view the response is depressed when the gaze is directed to make eye contact. The cell is thus sensitive to lateral aversion of both the eyes and the head.

DEFAULTING TO HEAD VIEW SENSITIVITY

There may be circumstances in which the gaze direction is not too clear. For example with strong lighting from above, the eyebrow ridges can cast a shadow over the eyes. In this case, the direction of attention can still be analysed (though perhaps with less certainty) from the direction in which the head is pointing. In these circumstances head angle could provide a useful "default." Cells showing combined sensitivity to the full face view (with the eyes occluded) and to eye contact (e.g., Figure 3) would thus be useful for signaling attention directed at the viewer in a variety of viewing conditions. Similarly, cells sensitive to both the profile view and averted gaze (e.g., Figure 6) would be useful for specifying averted attention under different lighting, etc.

ATTENTION DIRECTED UP OR DOWN

As mentioned above, sensitivity to head rotated away from the observer in the horizontal and vertical direction tended to be coded by separate cells. So too did coding of vertically and horizontally averted gaze. With gaze directed upwards, the cell in Figure 7 responded more to the face and to the face rotated upwards than to the same views with the eyes directed to make eye contact ($p < .02$). The cell also responded more to the profile turned upward than to the profile viewed in its normal orientation ($p < .02$) (overall effect of conditions: $F(7,36) = 17.6$, $p < .0001$; $N = 8, 4, 5, 6, 3, 7, 4, 7$). The cell is not simply coding head or eyes "turned away" since it does not respond to the profile face or to the face rotated downward.

If it is assumed that the function of the cell's responses is to provide an indication that another individual is directing attention to some place in the air, above the observer's head, then other aspects of

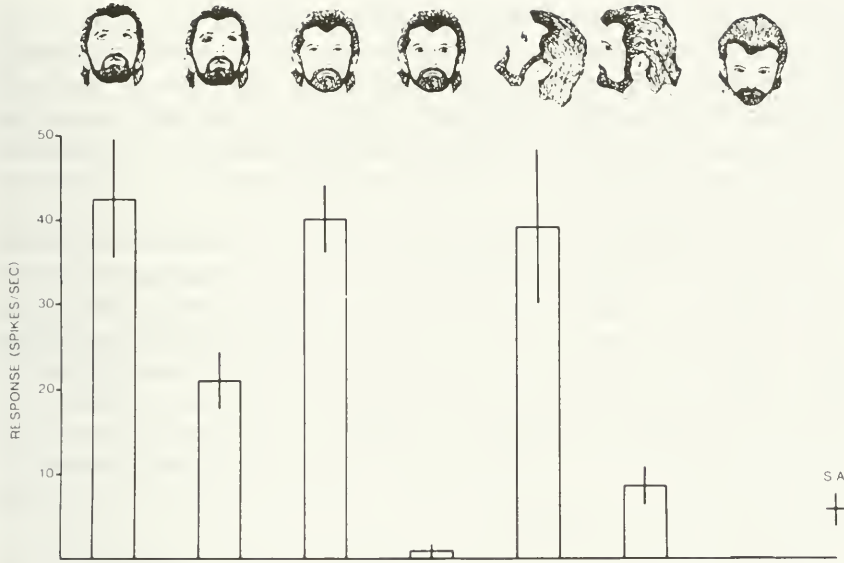


FIGURE 7. Sensitivity to head and gaze directed up. Upper: schematic representation of stimuli used for testing. Lower: mean and standard error of response of one cell (A078) to the stimuli. [$N = 8, 4, 5, 6, 3, 7, 4, 7$].

the cell's response make sense. While the cell does not respond to the full profile in its normal orientation, it does respond to the profile rotated upwards. The upward pointing profile would indicate that the individual being viewed is directing attention upwards.

When we consider gaze direction it is notable that the cell is unresponsive to both the full face and the face rotated upwards when the gaze is directed to make eye contact with the observer. For these stimuli the gaze angle gives a good indication that attention is not directed upwards but is directed at the observer. On the other hand, the cell does respond to both the full face view and the face turned upwards when the eyes are raised upward. Thus the cell responds to the sight of eyes raised upwards independent of the head view.

OBJECT CENTRED ANALYSIS

Gaze direction and head view can be analysed with different frames of reference. There are three main reference systems potentially applicable here (Feldman, 1985). These are the viewer, the object or individual under observation, and some part of the environment. Using the viewer or part of the environment as frames of

reference to interpret the cell's selectivity provides simple accounts of the function of the cells. A cell preferring head up may be coding attention above the viewer or attention in the upper part of the environment. A cell preferring left profile may be coding attention to the viewer's left or attention to a point in the environment (that happens to be on the viewer's left). We have yet to determine which description is more applicable.

Using the object as a frame of reference (an object centred analysis) is more complicated and appears less applicable to the results. This analysis utilizes the principal axis of the object or individual under observation as the frame of reference (Marr & Nishihara, 1978; Marr, 1982). For the cell (in Figure 7) responding to the face or profile with head raised, the angle of the head can be referenced to the torso. Under this scheme one might interpret the cell's activity as coding neck extension; the cell responding to all views of the body where the neck is extended away from the chest. This account does not explain the sensitivity to gaze direction.

For the same cell, attempts to relate the direction of gaze to the head viewed (also an object centred analysis) fail to produce a consistent description of the selectivity for gaze with different head angles. For the head level the cell responded well to the eyes directed upwards in their sockets but not to the eyes in the mid position of their sockets looking straight ahead. One might therefore conclude that the cell is coding eyes upward in their sockets. This account fails for two reasons. Firstly, the eyes in their mid socket position worked well when the head was raised. Secondly, the account predicts that the head lowered with direct eye contact (a posture commonly used as a threat signal) should activate the cell, since the eyes would be directed upwards in their sockets and would make eye contact with the observer. The cell, however, failed to respond to this configuration (data not illustrated).

DISCUSSION OF SENSITIVITY TO HEAD POSTURE AND GAZE DIRECTION

It is clear that the cells in the STS can supply information about the relative orientation of the head with respect to the viewer. The coding seems to be along two dimensions, corresponding to the degree of rotation towards or away from the observer in the horizontal and vertical planes. These two axes of analysis correspond to those noted to be most important in the neuronal coding of limb and head articulation (Perrett et al., 1985b, 1990a, 1990b).

In earlier studies, cells seemed to be insensitive to mirror reflection, responding equivalently to left and right profiles. Our more re-

cent studies indicate that a large number of cells are sensitive to the difference between mirror images and are selectively responsive to the head turned some angle laterally away from the viewer to one side only (Perrett et al., 1990b). [The left and right views of a real head may be slightly different but selective responses can be found with left and right mirror images of the same photographic slide (Perrett et al., 1989a, 1989c)]. Such left/right specificity is necessary if the function of the cells is to analyze direction of attention. By contrast, the separate coding of left and right profile views is unnecessary for object recognition because these mirror images have very similar visual characteristics.

In the vertical plane the majority of coding appears to generalize across different perspective views in the horizontal plane. As we have previously suggested, such generalization could be formed by the convergence of outputs of several different cells, each tuned to one horizontal view of the head with head raised posture. Indeed, such a convergence of information would seem to be a logical necessity since the visual cues defining head up posture are different for the face, profile, and back views. Some evidence in favour of this hierarchical scheme comes from the finding of a few cells that respond only to the head down from one view in the horizontal plane, e.g., left profile view with the head down.

The generalization of coding for head up or head down across a range of horizontal views of the head is interesting. The functional significance could reflect the fact that if an observer wants to direct his/her own attention to the point that another individual is attending, then all views with the head (and eyes) raised need the same behavioural response. If the observer sees a face turned up or a profile turned up or even the back of an individual's head turned up, then in each case, the observer needs to raise his or her own eyes to find what the other individual is looking at, or to what the individual is attending. Similarly, sight of a head (and eyes) down whether seen from the front, side, or back indicates a focus of another individual's attention in some lower part of the visual field.

The functional interpretation based on analysis of where an individual's attention is directed also accounts for the independent sensitivity to head posture and gaze direction displayed by some cells. Cells preferring the face turned to the observer also preferred the eyes to be turned towards the observer; cells preferring a laterally averted head posture also preferred laterally averted gaze and cells preferring a head posture raised in the air also preferred gaze directed upwards.

From the various populations of cells responsive to the sight of the head, the STS can code head posture and gaze direction of other individuals. These cellular mechanisms could have a role in social

behaviour. We have argued that one important function of the cells is to provide information about the focus of attention of other individuals. They thus provide answers to the questions "is that individual looking at me?" and if not "to where in the environment is that individual attending?"

II. PREDICTING THE CONSEQUENCES OF ONE'S OWN ACTIONS: STUDIES OF POLYSENSORY UNITS IN THE TEMPORAL CORTEX

The same brain region containing cells responsive to faces also contains cells responsive to somatosensory stimuli. In the upper bank of the STS of anaesthetized macaque monkeys Gross and his colleagues (Gross et al., 1981; Desimone & Gross, 1979; Bruce et al., 1981) found that tactile receptive fields were very large, often covering the whole body. Responses to tactile stimuli were extremely sensitive (detecting the displacement of a single hair) but were not selective for the nature of the tactile stimulus. Responses were usually transient in nature and were nonhabituating. A high proportion of cells with tactile responses were also responsive to visual stimuli. Bruce et al. (1981) found that the visual responses of such bimodal cells occurred over extremely large receptive fields (often cells would respond to stimuli throughout the entire visual field). Different classes of visual responses were observed, the majority preferred moving stimuli but were unselective for the form of the moving stimulus.

As discussed in the first part of this paper, the upper bank of the STS is known from a number of studies to contain populations of unimodal visual cells which exhibit a very high degree of selectivity, responding only to the sight of heads, or particular body movements. The cells with selective visual responses are not uniformly distributed in the STS but exist in patches (Perrett et al., 1985a). This patchy organization of physiological properties may coincide with the patchy anatomical distribution of input and output connections with this region (Seltzer & Pandya, 1984; Harries & Perrett, 1989; & D.N. Pandya, personal communication). It is possible that selective visual neurons and unselective polymodal neurons exist in different patches within the same cortical area.

Given the high degree of visual selectivity exhibited by cells responsive to the head, the apparent lack of selectivity exhibited by the cells processing somatosensory information and visual motion is surprising. This discrepancy was the main motivation for the present study. We reasoned that a re-examination of somatosensory coding in awake, behaving monkeys might reveal selectivity in the processing which is not apparent in the anaesthetized state. Cells selective for visual stimuli in the upper bank of the STS (area TPO of Seltzer &

Pandya, 1978) are responsive to stimuli originating from other individuals. For example, cells selective for faces or body movements respond to the sight of faces and movements of other individuals. The visual processing could be construed as providing information useful in social or predator/prey interactions.

SOMATOSENSORY PROCESSING

Somatosensory processing in TPO could be signalling the presence of others in the same way as visually responsive cells. In anaesthetized monkeys all stimulation is derived passively from other individuals (the experimenters). This reasoning led us to investigate what would happen in the awake, behaving state when the monkey actively caused the tactile stimulation by, say, touching itself.

With anaesthetized monkeys it is only possible to measure the effect of "passive" tactile stimulation, that is, stimulation which does not arise "actively" through the monkey's own movements. Such passive stimulation, when conducted out of sight, is inherently unpredictable in nature. In the awake behaving state, active tactile exploration (out of sight) can lead to both predictable and unpredictable stimulation. Encountering a familiar object in a familiar location (for example, one's own body surface) produces predictable sensations, whereas encountering objects which have been placed within reach without one's knowledge produces unpredictable sensations.

During the investigation it became apparent that STS neurons were dependent on whether stimuli could be "expected." Neurons discharged to somatosensory stimuli only when stimulation was unexpected. A study was therefore made investigating the relationship between the activity of the neurons and the predictability of the tactile stimulus based on other sources of tactile or visual information. The results of the study have been described in brief (Mistlin et al., 1986; Chitty et al., 1986; Perrett et al., 1989d) and are the subject of a fuller report (Mistlin & Perrett, 1990).

METHODS

As explained above, passive stimulation out of sight is unpredictable and unexpected. We arranged unexpected active stimulation to occur by placing novel textures (wood, fur, metal) on some part of the primate chair which the monkey frequently explored (e.g., the foot perch), or in some part of space that the monkey would encounter during its movements. Tactile stimulation out of sight was also compared to stimulation in sight with the monkey able to see the object causing tactile contact.

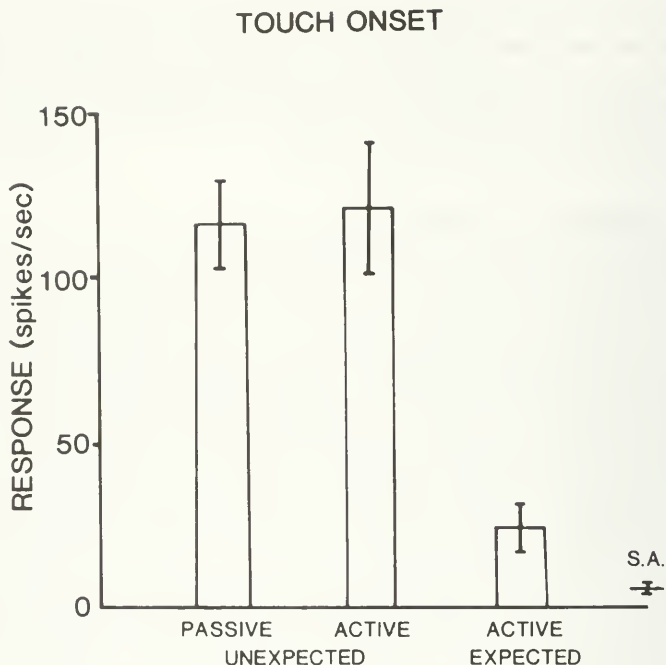


FIGURE 8. Comparison between response to expected and unexpected tactile stimulations. The mean and standard error of response is illustrated for one cell (F026). $N = 5, 5, 6, 8$.

RESULTS

Tactile Stimulation out of Sight

Testing with passive tactile stimulation revealed results that were similar to those obtained in the anaesthetized state. We found that cells responsive to somatosensory stimuli had very large receptive fields covering most of the body. The cells also displayed an apparent lack of stimulus selectivity responding to tactile contact with any stimulus (wood, fur, metal, etc.).

Figure 8 illustrates the results for one cell typical of those studied. It gave a large response when the monkey was touched by the experimenter (passive touch). Here the stimulation was inherently unpredictable. By contrast the cell was completely unresponsive when the monkey touched itself or a familiar part of the primate chair (active touch) (overall effect of conditions: $F(3,20) = 32.6, p < .01$; $N = 5, 5, 6, 8$). Differences between responses to active and passive

stimulation can not be accounted for in terms of differences in pressure or area of skin stimulated because careful attention was given to ensure that stimulation was comparable. Furthermore, the cell responded to touch across a range of tactile pressures and across a range of positions over the body.

The monkey's own movements can also lead to unexpected stimulation. When the monkey explored the environment out of sight and encountered a novel object, then tactile stimulation was unexpected and the cell illustrated in Figure 8 responded. Thus, the important dimension was whether the stimulation was predictable and not whether the stimulation was active or passive.

Eighty-five cells were studied with expected and unexpected tactile stimulation arising actively or passively. The majority of cells (94%) did not respond above spontaneous activity when the monkey touched itself or any familiar part of the chair but were responsive when the monkey touched unexpected surfaces or was touched unexpectedly by the experimenter.

What is remarkable is that at the level of the primary sense organs, sensations arising from expected and unexpected surfaces could be identical, yet the STS cells respond only to unexpected sensations. For example, the monkey's paw touching fur at an unexpected place and the monkey touching its own leg would produce very similar somaesthetic stimulation of the skin, yet STS cells responded only to the former stimulus.

The generality of response to passive tactile stimulation with any type of material can mislead one into thinking that the somatosensory processing in the STS does not discriminate texture. The activation of somatosensory cells in the STS must depend on a mismatch between the tactile qualities of the surfaces that the monkey expects to encounter and the tactile qualities which actually arise at a given position. The fact that the cells do not respond to the tactile contact of an expected surface means that the cells (or mechanisms antecedent to them) have processed the physical properties of the surface (texture and hardness) and found them to match expected properties. Thus, the cells are selective for tactile texture but selectivity is conditional on spatial position and expectation of the stimulus at that position.

Tactile Stimulation in Sight

All the testing described above was conducted out of sight and thus visual information could not be used by the monkey to make any intermodal predictions about the occurrence and nature of the tactile stimulation. We have compared the responsiveness of 30 cells to tactile stimulation in and out of sight. For passive tactile contact the majority of cells' responses (70%) were significantly reduced when the

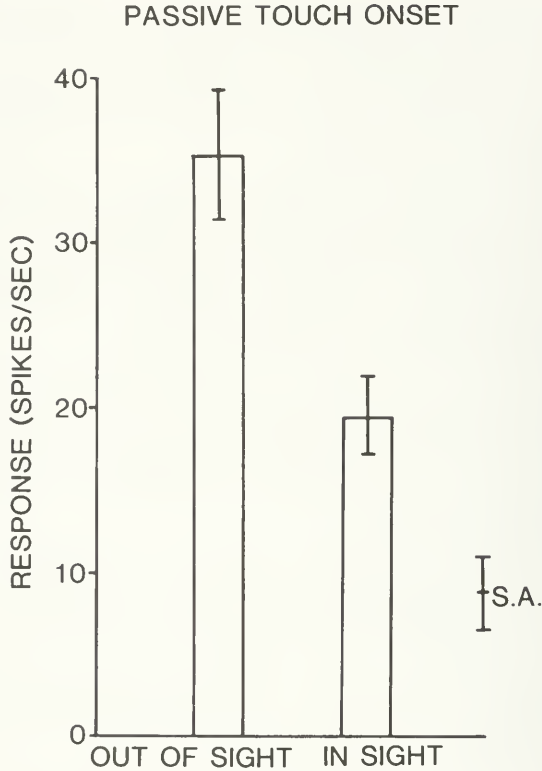


FIGURE 9. Comparison between passive tactile contact in sight and out of sight. The mean response and standard error of response for one cell (F123A) is illustrated for different conditions. $N = 10$.

monkey could witness the trajectory of an object moving on a course which resulted in tactile contact, as compared with an equivalent tactile contact from unseen objects at the same location on the skin (Figure 9; $p < .05$, each comparison; overall effect of conditions: $F(2,17) = 78.7$, $p < .01$; $N = 10$). The remaining 30% of the cells responded without difference to tactile stimulation in and out of sight.

A similar effect of vision was found for active tactile stimulation — with cells being more responsive when the monkey's movements resulted in tactile contact with objects that were out of sight, as compared with equivalent tactile contact with the same objects that were visible.

Novelty

The cellular sensitivity to the expected/unexpected dimension in stimulation does not reflect sensitivity to novelty per se, since cells

showed little if any short term habituation. Thus cells responded consistently to passive stimulation over 10-50 consecutive repetitions (interstimulus interval = 2-5 s). Similarly for active stimulation, repeatable responses were obtained during repeated exploration of unexpected surfaces.

If an object remains in the immediate environment long enough, then at some stage it may come to be regarded as familiar and hence predictable. We have, however, not yet investigated the full time course of this transition in status from unexpected to expected.

WITNESSING ONE'S OWN MOVEMENT

The distinction between expected and unexpected stimulation discussed above for the tactile modality can also be found in the visual modality. In the visual modality the distinction has a longer history of theoretical consideration. Sperry (1950) introduced an idea that the motor centres, when sending motor commands for moving the eyes, also send a corollary discharge to the visual centres to compensate for the retinal displacement during these voluntary eye movements. According to this theory, corollary discharges were not restricted to only visual stabilization mechanisms, but they functioned as a "central adjustor factor" to ensure perceptual stability during self-induced actions.

Von Holst and Mittelstaedt (1950) distinguished between "reafferent" stimulation arising as a consequence of one's own actions and "exafferent" stimulation which arises as a consequence of changes in the environment unrelated to one's own actions. Like Sperry (1950) they proposed that an "efference" copy of the motor commands to move the eyes is sent to sensory structures to null the reafferent stimulation which arises from the eye movement. In normal circumstances, the efference copy matches and cancels the reafferent stimulation, but this does not happen when, for example, the eye muscles do not move in accordance with the motor commands to move them. When the eye muscles are paralysed attempts to move the eyes to the right result in an unpleasant sensation where the visual world moves to the right (Huglhings-Jackson, 1932).

Note that the distinction between reafferent and exafferent stimuli is not quite the same as the expected/unexpected dimension described for the somatosensory modality. In different situations passive (exafferent) tactile stimulation can be either expected or unexpected (being touched in sight or out of sight). Similarly, there are situations in which active (reafferent) tactile stimulation is predictable or unpredictable (touch self or touch novel object out of sight).

In the visual modality exafferent stimulation is mainly unex-

pected and reafferent stimulation is mainly expected. This is particularly true in the case of eye movements where the consequent retinal changes are largely predictable. There are, however, many more situations where reafferent visual sensations are predictable; in a familiar environment retinal image motion caused by head and body movement is also predictable. Furthermore, the visual changes which arise as one's own limbs move into and within view are also largely predictable.

We have begun to study the responsiveness of movement-sensitive cells in the STS to the sight of the monkey's own limbs moving. This testing has again revealed the complexity of response sensitivity which at first glance appeared rather nonspecific. There are a variety of motion sensitive cells in the area TPO of the STS; many are form-selective and respond only to the sight of particular body movements. Others, however, are not selective for form and respond to all objects moving independent of size and shape.

MOTION SENSITIVE CELLS UNRESPONSIVE TO SELF-PRODUCED MOTION

We have studied a variety of different types of motion-sensitive cells lacking form selectivity. These cell types were selective for movement upwards, movement towards the monkey, movement into view and movement in any direction. Since at the retinal level each of these classes of movement occurs when the monkey brings its hand to its mouth, a comparison can be made between reafferent stimulation (retinal image movement resulting from the monkey's own action) and comparable exafferent stimulation (retinal image movement resulting from the movement of some external object in the environment unrelated to the monkey's action).

So far in a study of 35 cells we have found 26 which discriminated self-produced movement from nonself-produced movement. These 26 cells responded well to the experimenter's hand being brought into view or to an object moved by the experimenter into view but were unresponsive to the sight of the monkey's own hand coming into view along the same trajectory. None of these cells which discriminated between movements of the experimenter's hand and the monkey's own hand, showed sensitivity to form, size, or velocity which could account for the difference in response. Indeed, the cells generalized their responses to movements of objects of different size, colour, etc. Nine cells studied showed no difference between the sight of self-produced movements and the sight of movements not produced by the monkey.

Figure 10 illustrates the responses of one cell sensitive to the

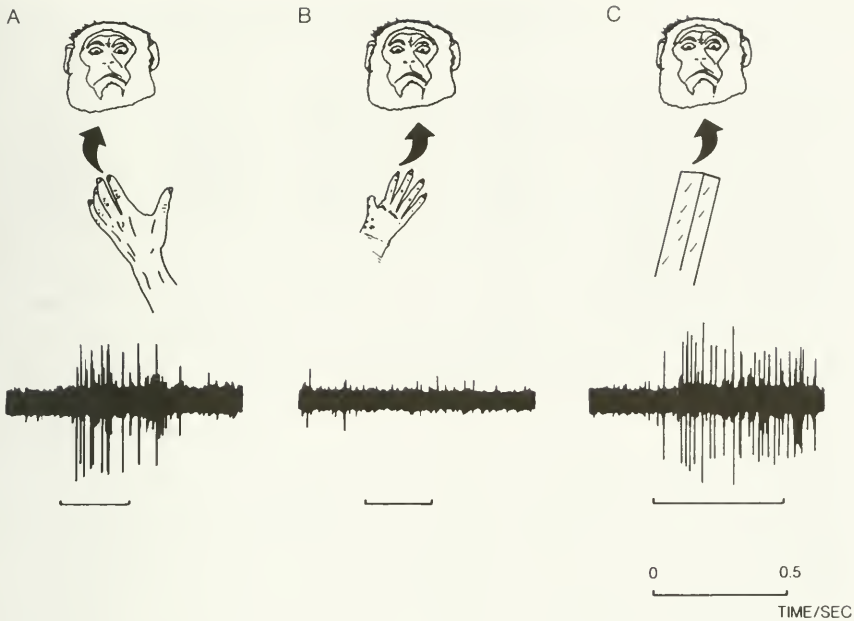


FIGURE 10. Motion sensitive cell unresponsive to the sight of own limb movement. Three trials with a human hand, the monkey's own hand, and a bar entering the field of view. Upper: stimuli illustrated schematically. Lower: traces of neuronal activity with the onset and duration of the moving stimuli marked by the horizontal line.

sight of stimuli moving upwards and into the field of view. This cell displayed a lack of form selectivity, responding when small objects, large objects, and the experimenter's hand were brought into view. When, however, the monkey brought its own hand into view, with or without small pieces of food, there was no response above spontaneous activity.

One might assume that the difference in conditions reflects different states of attention — the monkey paying little or no attention to its own hand but looking at and attending to other objects coming into view. This explanation is unlikely, first because video film reveals that the monkeys pay acute attention to their own hands when they bring food towards their mouths. Second, we have found that responses to a moving stimulus (other than the monkey's hands) occur even when the monkey is not looking directly at this moving stimulus (Perrett et al., 1985a). Measurements of receptive fields of motion-sensitive cells both in the anaesthetized preparation (Desimone et al., 1984) and in the awake monkey (Perrett et al., 1989a, 1989b; Perrett, Harries, & McHugh, unpublished studies) reveal that they are extremely large, usually extending more than 20° from the

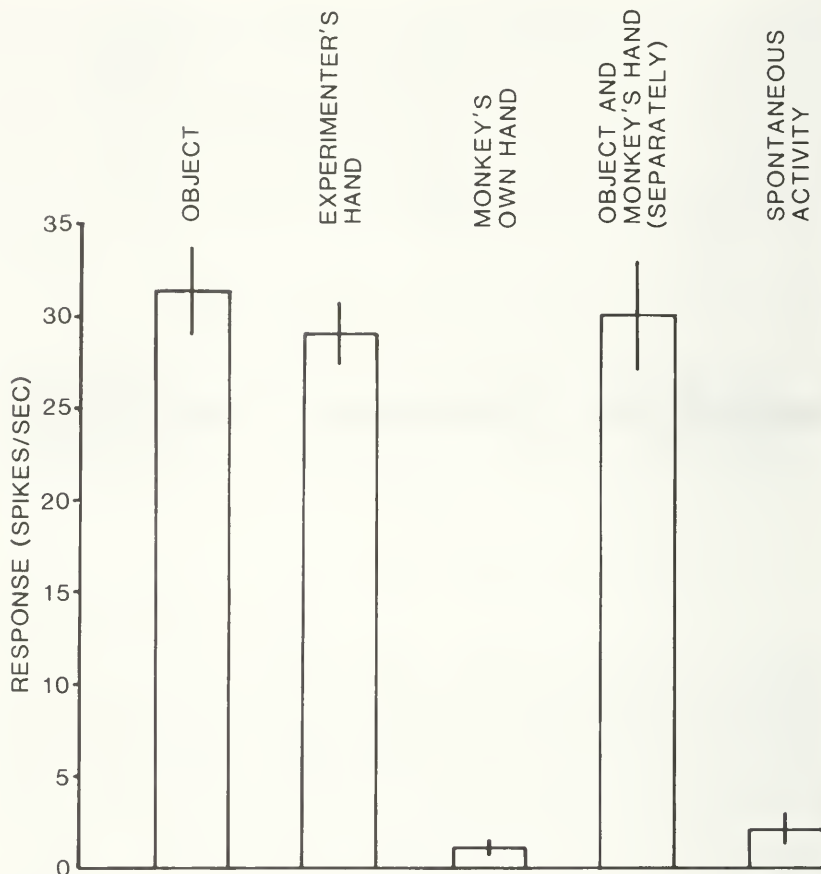


FIGURE 11. Quantitative comparison of self- and nonself-produced motion. The mean and standard error of one cell's responses are given to the sight of different stimuli moving into the field of view. $N = 14$.

fovea in all directions. Throughout these fields the cells are equivalently responsive to one type of movement. Thus, even if the monkey was not directly fixating on its own hand, one would still expect a neuronal response to hand movement because the movement would fall within the large receptive fields.

The absence of response to the monkey's own hand movement is not due to some general shut-down of motion processing during the hand movement. The cell illustrated in Figure 11 is more responsive to the sight of objects and the experimenter's hand moving into view than to the sight of the monkey's own hand moving into view or to spontaneous activity ($p < .01$, each comparison). The cell's response to objects moving into view was, however, unaffected by the simultaneous presence of the monkey's own hand in view (overall effect of conditions: $F(4,65) = 64.2$, $p < .01$; $N = 14$).

CAPACITIES NECESSARY FOR IGNORING THE SELF-PRODUCED SENSATIONS

It is interesting to consider what information would be necessary in order to ignore one's own limb movements. The process may involve information about the predicted or felt (perceived) position of the limbs, the predicted trajectory, velocity and direction of limb motion and the visual appearance of the limbs plus whatever they may be carrying. We have just begun to explore the ability of visually responsive cells in the STS to ignore self-produced movements and have not yet defined how this happens. So far, our studies only provide physiological evidence that expectations generated from an individual's limb movements do influence sensory processing of the sight of those movements.

A similar diverse set of information is needed to account for the difference between expected and unexpected tactile sensations. The lack of response to expected tactile stimulation indicates knowledge of the spatial lay-out of the immediate space around the subject, knowledge of the tactile properties of all surfaces within this space, information about the current position, and predicted trajectory of limb movement.

At the most general level, an animal must be attuned to sensory events which indicate the actions of other animals but this can only be achieved by being able to ignore the sensory events which arise from the animal's own actions. The response properties of cells in the STS show that there are neural mechanisms sensitive to the predictable consequences of an individual's actions in the visual and tactile modalities. Predictable reafferent stimulation in visual and tactile modalities is effectively ignored by the majority of the neurons in the STS. This allows unexpected stimulation to be selectively detected.

The effect of expectation is not restricted to reafferent stimulation. Even with sensory information arising from changes in the environment that are unrelated to the monkey's own actions, we find that expectations set up on the basis of information from one modality can be used to null or attenuate processing of sensory information in a second modality. Hence the sight of an object moving on a course likely to contact the skin surface can attenuate the neuronal responses to the tactile stimulation at contact.

CONCLUSION

The three types of stimuli processed in the STS that have been discussed here have in common the fact that they are all potent in releasing orienting responses. Reflection on one's own experience makes this obvious. Faces, particularly those making eye contact are

extremely arousing stimuli. You soon become aware when someone is looking at you. Similarly, in the tactile modality it is very difficult to ignore a tactile stimulus that arises when someone or something unexpectedly touches you, whereas equivalent tactile stimulation arising when you touch yourself or some known surface goes largely unnoticed. Similarly we are not startled by the sight of movements of our own hands but we are likely to be alerted by other stimuli moving into view, particularly when these are close to our body.

Since unpredictable sensations often arise from other animals, the STS area appears well suited to defining sensory stimuli that are important in social or predator/prey interactions.

In general, sensory effects which are the predictable results of one's own actions do not need attention but (like faces) visual movements and tactile stimuli that are unexpected usually require behavioural reactions. The capacity to ignore self-produced sensations when they are predictable is a capacity which relies on an internal representation of the local environment from which to make predictions as to how sensory input from the environment will alter as a result of the organisms own actions. This type of assertion has frequently been suggested from psychological considerations (Gregory, 1980; MacKay, 1973) but as yet there has been little physiological evidence for the role of expectation and prediction in sensory information processing.

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REFERENCES

- Aggleton, J.P., Burton, M.J., & Passingham, R.E. (1980). Cortical and subcortical afferents to the amygdala of the rhesus monkey (*Macaca mulatta*). *Brain Research*, 190, 347-368.
- Argyle, M., & Cook, M. (1975). *Gaze and mutual gaze*. Cambridge, UK: Cambridge University Press.
- Baylis, G.C., Rolls, E.T., & Leonard, C.M. (1985). Selectivity between faces in the responses of a population of neurons in the cortex of the superior temporal sulcus of the macaque monkey. *Brain Research*, 342, 91-102.
- Baylis, G.C., Rolls, E.T., & Leonard, C.M. (1987). Functional subdivisions of the temporal lobe neocortex. *Journal of Neuroscience*, 7, 330-342.

- Bell, C.C. (1989). Sensory coding and corollary discharge effects in mormyrid electrical fish. *Journal of Experimental Biology*, *146*, 229-253.
- Bertrand, M. (1969). The behavioural repertoire of the stump-tail macaque: A descriptive and comparative study. *Bibliotheca Primatologica*, *11*. Basel: Krager.
- Bruce, C.J., Desimone, R., & Gross, C.G. (1981). Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *Journal of Neurophysiology*, *46*, 369-384.
- Chance, M.R.A. (1962). An interpretation of some agonistic postures: The role of 'cut-off' acts and postures. *Symposia Zoological Society London*, *8*, 71-99.
- Chitty, A.J., Mistlin, A.J., & Perrett, D.I. (1985). Somatosensory and associated visual properties of neurons in a polysensory region of macaque temporal cortex. *Journal of Physiology*, *367*, 28P.
- Desimone, R., Albright, T.D., Gross, C.G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, *8*, 2051-2062.
- Desimone, R., & Gross, C.G. (1979). Visual areas in the temporal cortex of the macaque. *Brain Research*, *178*, 363-380.
- Feldman, J.A. (1985). Four frames suffice: A provisional model of vision and space. *Behavioural and Brain Sciences*, *8*, 265-289.
- Galletti C., Battaglini, P.P., & Aicardi, G. (1988). 'Real-motion' cells in visual area V2 of behaving macaque monkeys. *Experimental Brain Research*, *69*, 279-288.
- Gregory, R. (1980). Perceptions as hypotheses. *Philosophical Transactions of the Royal Society of London*, *B*, *290*, 181-197.
- Gross, C.G., Rocha-Miranda, C.E., & Bender, D.B. (1972). Visual properties of neurons in the inferotemporal cortex of the macaque. *Journal of Neurophysiology*, *35*, 96-111.
- Harries, M.H., & Perrett, D.I. (1991). Visual processing of faces in the temporal cortex: Physiological evidence for a modular organization and possible anatomical correlates. *Journal of Cognitive Neuroscience*, *3*, 9-24.
- Hasselmo, M.E., Rolls, E.T., Baylis, G.C., & Nalwa, V. (1989). Object centred encoding by face selective neurons in the cortex in the superior temporal sulcus of the monkey. *Experimental Brain Research*, *75*, 417-429.
- Hikosaka, K., Iwai, E., Saito, H.A., & Tanaka, K. (1989). Polysensory properties of neurons in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. *Journal of Neurophysiology*, *60*, 1615-1635.
- Hinde, R.A., & Rowell, T.E. (1962). Communication by posture and facial expressions in the rhesus monkey (*Macaca mulatta*). *Proceedings of the Zoological Society of London*, *138*, 1-21.
- Holst, E., von, & Mittelstaedt, H. (1950). Das reafferenzprinzip (Wechselwirkungen zwischen zentralnervensystem und peripherie). *Naturwissenschaften*, *37*, 464-476.
- Hoof van, J.A.R.A.M. (1967). Facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7-68). London: Weidenfeld and Nicolson.
- Hughlings-Jackson, J. (1932). *Selected writings: Vol. 2*. London: Hodder and Stoughton.
- Hyvärinen, J., & Poranen, A. (1974). Function of the parietal associative area 7 as revealed from cellular discharges in alert monkeys. *Brain*, *97*, 673-692.
- Jones, E.G., & Powell, T.P.S. (1970). An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. *Brain*, *93*, 793-820.
- Leinonen, L., Hyvärinen, J., Nyman, G., & Linnankoski, I. (1979). Functional properties of neurons in lateral part of associative area 7 in awake monkey. *Experimental Brain Research*, *34*, 299-320.
- Lynch, J.C., Mountcastle, V.B., Talbot, W.H., & Yin, T.C.T. (1977). Parietal lobe mechanisms for directed visual attention. *Journal of Neurophysiology*, *40*, 362-389.
- MacKay, D.M. (1973). Visual stability and voluntary eye movements. In R. Jung (Ed.), *Handbook of sensory physiology: Vol VII/3A* (pp. 307-332). Berlin: Springer Verlag.
- Marr, D. (1982). *Vision*. San Francisco: W.H. Freeman & Co.
- Marr, D., & Nishihara, N.K. (1978). Representation and recognition of the spatial organization of three-dimensional shapes. *Proceedings of the Royal Society of London*, *B*, *200*, 269-294.
- Mistlin, A.J., & Perrett D.I. (1990). Visual and somatosensory processing in the

- macaque temporal cortex: The role of expectation. *Experimental Brain Research*, *82*, 437-450.
- Mistlin, A.J., Perrett, D.I., & Chitty, A.J. (1986). Somatosensory and associated visual properties of neurons in a polysensory region of macaque temporal cortex: A preliminary study. *Behavioural Brain Research*, *20*, 120.
- Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., & Acuna, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology*, *38*, 871-908.
- Perrett, D.I., Rolls, E.T., & Caan, W. (1982). Visual neurons responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, *47*, 329-342.
- Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., & Jeeves, M.A. (1984). Neurons responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. *Human Neurobiology*, *3*, 197-208.
- Perrett, D.I., Smith, P.A.J., Potter, D.D., Mistlin, A.J., Head, A.S., Milner, A.D., & Jeeves M.A. (1985a). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London B*, *223*, 293-317.
- Perrett, D.I., Smith, P.A.J., Mistlin, A.J., Chitty, A.J., Head, A.S., Potter, D.D., Broennimann, R., Milner, A.D., & Jeeves, M.A. (1985b). Visual analysis of body movements by neurons in the temporal cortex of the macaque monkey: A preliminary report. *Behavioural Brain Research*, *16*, 153-170.
- Perrett, D.I., Mistlin, A.J., & Chitty, A.J. (1987). Visual cells responsive to faces. *Trends in Neuroscience*, *10*, 358-364.
- Perrett, D.I., & Harries, M.H. (1988). Characteristic views and the visual inspection of simple faceted and smooth objects: 'tetrahedra and potatoes'. *Perception*, *17*, 703-720.
- Perrett, D.I., Mistlin, A.J., Chitty, A.J., Smith, P.A.J., Potter, D.D., Broennimann, R., & Harries, M.H. (1988). Specialized face processing and hemispheric asymmetry in man and monkey: Evidence from single unit and reaction time studies. *Behavioural Brain Research*, *29*, 245-258.
- Perrett, D.I., Mistlin, A.J., & Harries, M.H. (1989a). Seeing faces: The representation of facial information in temporal cortex. In J.J. Kulikowski, C.M. Dickinson, & I.J. Murray (Eds.), *Seeing contour and colour* (pp 740-754). Oxford: Pergamon Press.
- Perrett, D.I., Harries, M.H., Mistlin, A.J., & Chitty, A.J. (1989b). Recognizing objects and actions: Frameworks for neuronal computation and perceptual experience. In D.M. Guthrie (Ed.), *Higher order sensory processing and artificial sensing* (pp 155-173). Manchester, UK: Manchester University Press.
- Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.J., Hietanen, J.K., & Ortega, J.E. (1989c). Frameworks of analysis for the neural representation of animate objects and actions. *Journal of Experimental Biology*, *146*, 87-113.
- Perrett, D.I., Mistlin, A.J., Harries, M.H., & Chitty, A.J. (1989d). Understanding the visual appearance and consequence of hand actions. In M.A. Goodale (Ed.), *The control of grasping* (pp. 163-188). Norwood, NJ: Ablex Press.
- Perrett, D.I., & Mistlin A.J. (1990). Perception of facial attributes. In W.C. Stebbins & M.A. Berkley (Eds.), *Comparative perception: Vol. II. Complex signals* (pp. 187-215). New York: John Wiley & Sons.
- Perrett, D.I., Harries, M.H., Benson, P.J., Chitty, A.J., & Mistlin, A.J. (1990a). Retrieval of structure from rigid and biological motion; an analysis of the visual response of neurons in the macaque temporal cortex. In T. Troscianko & A. Blake (Eds.), *AI and the eye* (pp 181-201). Chichester: John Wiley & Sons.
- Perrett, D.I., Harries, M.H., Chitty, A.J., & Mistlin, A.J. (1990b). Three stages in the classification of body movements by visual neurons. In H.B. Barlow, C. Blakemore, & M. Weston-Smith (Eds.), *Images and understanding* (pp. 94-107). Cambridge UK: Cambridge University Press.
- Perrett, D.I., Oram, M.O., Harries, M.H., Bevan, R., Hietanen, J.K., Benson, P.J., & Thomas, S. (in press). Viewer-centred and object-centred encoding of heads by cells in the superior temporal sulcus of the rhesus monkey. *Experimental Brain Research*.

- Redican, W.K. (1975). Facial expression in non human primates. In L.A. Rosenblum (Ed.), *Primate behaviour: Vol. 4* (pp. 103-194). New York: Academic Press.
- Rolls, E.T. (1984). Neurons in the cortex of the temporal lobe and in the amygdala of the monkey selective for faces. *Human Neurobiology*, 3, 209-222.
- Rolls, E.T., & Baylis, C.G. (1986). Size and contrast have only small effects on the responses to faces of neurons in the cortex of the superior temporal sulcus of the macaque monkey. *Experimental Brain Research*, 65, 38-48.
- Seltzer, B., & Pandya, D.N. (1978). Afferent cortical connections and architectonics of the superior temporal sulcus and surrounding cortex in the rhesus monkey. *Brain Research*, 149, 1-24.
- Seltzer, B., & Pandya, D.N. (1984). Further observations on parieto-temporal connections in rhesus monkeys. *Experimental Brain Research*, 55, 301-312.
- Sperry, R.W. (1950). Neural basis of the spontaneous optokinetic response produced by visual neural inversion. *Journal of Comparative and Physiological Psychology*, 43, 482-489.
- Wallace, H. (1985). Perceiving a stable environment. *Scientific American*, 252, 92-98.

