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Organization and Functions of Cells Responsive to Faces in the Temporal Cortex [and Discussion]

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Organization and functions of cells responsive to faces in the temporal cortex

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SUMMARY

Cells selectively responsive to the face have been found in several visual sub-areas of temporal cortex in the macaque brain. These include the lateral and ventral surfaces of inferior temporal cortex and the upper bank, lower bank and fundus of the superior temporal sulcus (STS). Cells in the different regions may contribute in different ways to the processing of the facial image.

Within the upper bank of the STS different populations of cells are selective for different views of the face and head. These cells occur in functionally discrete patches (3–5 mm across) within the STS cortex. Studies of output connections from the STS also reveal a modular anatomical organization of repeating 3–5 mm patches connected to the parietal cortex, an area thought to be involved in spatial awareness and in the control of attention.

The properties of some cells suggest a role in the discrimination of heads from other objects, and in the recognition of familiar individuals. The selectivity for view suggests that the neural operations underlying face or head recognition rely on parallel analyses of different characteristic views of the head, the outputs of these view-specific analyses being subsequently combined to support view-independent (object-centred) recognition.

An alternative functional interpretation of the sensitivity to head view is that the cells enable an analysis of 'social attention', i.e. they signal 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 directed to the observer's left. Such information is useful for analysing social interactions between other individuals. This interpretation accounts not only for the extensive tuning to head view in the horizontal plane, but also explains the additional tuning of many STS cells to gaze direction and vertical elevation of the head and body posture. Deficits in perception of gaze direction after lesions to the macaque STS cortex, and in certain cases of prosopagnosia, are also predicted by this interpretation.

1. INTRODUCTION

In 1972, cells selectively responsive to faces in the temporal cortex of monkeys were reported (Gross *et al.* 1972). Such cells have been defined as selective for faces because they do not respond to a variety of other types of stimuli (including simple or complex visual patterns that are neutral or arousing, such as snakes or bananas). Despite the length of time since their first discovery, experimental study of such cells is still a relatively new endeavour. For the first ten years experimental reports were brief and were subject to much scepticism. During the 1980s, study of the cells began in earnest in at least six laboratories. Such physiological study is still limited when compared with the mass of psychological, neurological and computational studies of face recognition.

Here we consider briefly the ways that the physiological study of face processing can guide and test psychological and computational theories. We also discuss a new functional interpretation of cells responsive to faces, and integrate physiological data with neuropsychological studies of face processing deficits after brain damage.

2. SENSITIVITY TO PERSPECTIVE VIEW

Cells in the temporal cortex of monkeys, which respond selectively to hands, faces and other classes of biologically significant stimuli, such as body movements and actions, provide an opportunity to investigate directly the manner in which objects are represented in the nervous system.

Early studies showed that cells responsive to the sight of the head were selective for perspective view; some cells responded to the full face, other cells responded to the profile (Perrett *et al.* 1985; Desimone *et al.* 1984). A recent study (Perrett *et al.* 1991*a*) has confirmed that the majority of cells in the superior temporal sulcus (STS) (110 out of a sample of 119 responsive to the head) exhibit view selectivity. The same cells have been found to generalize response to one view of the head across image position, size, orientation and different lighting conditions (Perrett *et al.* 1982, 1984, 1989). Cells tuned to one view can therefore be seen as providing a high level 'viewer-centred' description covering almost all instances of that view. Such properties contradict computational models of recognition (Marr & Nishihara 1978; Lowe

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1987), in which low level representations of surfaces or edge features are mapped directly onto three-dimensional representations of objects which generalize across all views.

(*a*) *Characteristic views for recognition*

As the cells in the temporal cortex are selective for a given view of the head, the question arises as to how many separate views of the head are represented by the cells in the cortex. Are all views represented evenly, or are particular 'characteristic' views preferentially coded as some theoretical accounts of recognition suggest (Koenderink & van Doorn 1979)? The selective representation of particular views in memory presents an efficient or economic way of coding the appearance of an object for recognition (for review, see Perrett *et al.* (1991*b*)).

An early survey of the view tuning of STS cells (Perrett *et al.* 1985) suggested coding of just four views in the horizontal plane (namely the face, left and right profile and back view). Later studies showed that more views were coded than just these four (Perrett *et al.* 1989, 1991*a*; Hasselmo *et al.* 1989). Recent analysis of 119 cells responsive to the head revealed that, although cells were tuned to a whole range of views in the horizontal plane, there was an overall statistical preference for face, profile and back view compared with intermediate views (Perrett *et al.* 1991*a*; Harries & Perrett 1991).

This neurophysiological evidence for the importance of particular head views parallels the importance of different views that has been found in behavioural studies (Harries *et al.* 1991; Perrett *et al.* 1991*b*). In both types of study, the face and profile views appear to be more important than half-profile views, but all of these front views are more important than the rear views of the head. Together the results support models of face and object recognition based on selective representation of characteristic views (Perrett *et al.* 1991*b*; Perrett & Harries 1988).

(*b*) *Tolerance of non-optimal views*

If cells preferentially code only a few characteristic views then cell tuning for perspective views needs to be broad to accommodate views in between the characteristic views. Measurements made on a sample of 73 cells suggested that, on average, responses declined to half-maximal response for a rotation of the head 60° from the cell's optimal view (Perrett *et al.* 1989, 1991*a*). Thus, cells tuned to the face will be half activated by the sight of a view of the head rotated towards the profile by 60°. With this broad view tuning, selective coding of the four characteristic views can cover the whole range of perspective views in the horizontal plane. This would be analogous to the retinal basis of colour vision, where just three types of receptor, each type broadly tuned to wavelength, provide information about all visible wavelengths.

(*c*) *Links with identity priming in face recognition*

Most cells selective for faces respond equally to the heads of different individuals, but about 10% show an additional sensitivity for the identity of familiar faces (Perrett *et al.* 1984, 1987, 1989, 1991*a*; Baylis *et al.* 1985). Most of these cells exhibit view-selective coding, suggesting that recognition of a familial individual is also based on a small number of characteristic views of that person held in memory.

The time taken to recognize a picture of a familiar face is shorter when the picture has been presented before (Bruce & Young 1986). This identity or repetition priming is weak between dissimilar perspective views of the same face, and does not occur between the images of a person's face and his or her body (Ellis *et al.* 1987). Priming does, however, occur between one visual region of the face to a second region of the same face (Brunas *et al.* 1990).

If one assumes that repetition of an image results in more efficient activation of identity-sensitive cells (or a more efficient link between the cells and contextual cues), then the generalization properties of priming are predictable from the cell properties. Most of the identity-sensitive cells are view specific, do not respond to both the head and body, but are sensitive to multiple features of the head (Perrett *et al.* 1984, 1989, 1991*a*).

(*d*) *Formation of object-centred descriptions*

Although most cells responsive to faces in the STS tolerate a limited range of viewpoints, we suggested (Perrett *et al.* 1984, 1985, 1987) that their outputs could be combined hierarchically to enable cells 'upstream' to generalize across all viewpoints. Recent computational (Seibert & Waxman 1991; Ullman 1989) and artificial neural net models of recognition (Poggio & Edelman 1990) follow the suggested hierarchical scheme and use viewer-centred descriptions as an intermediate stage for establishing view independent object recognition.

A few cells (e.g. 4% of cells responsive to the head, reported by Perrett *et al.* 1991*a*) in the temporal cortex exhibit object-centred properties and do respond to multiple views of the head or body (Hasselmo *et al.* 1989; Perrett *et al.* 1984, 1985, 1987, 1989, 1990, 1991*a*). The hierarchical scheme suggested above predicts that the response latency of such view-independent cells should be longer than that for view-specific cells. Cells responsive to all views proved to be rare, but comparisons between the two types of cells recorded in the same experimental subject confirmed that the mean latency of object-centred cells (130 ms, $n = 6$) was significantly greater than that for viewer-centred cells (119 ms, $n = 37$, $t = 2.98$, d.f. $= 26$, $p < 0.01$, Satterthwaite approximation for degrees of freedom).

The small (11 ms) time difference between activation of viewer- and object-centred cells may reflect the fact that the pooling of information across views can occur across one synapse. (It takes about 5 ms for one cell to excite a second cell.) In retrospect, this small time difference means that the endeavour to confirm the hierarchical model using response latencies was ambitious. The results are therefore gratifying.

3. SOCIAL ATTENTION

Virtually all studies of cells responsive to faces have been made with the assumption that the cells are involved in the recognition of faces as one class of object or as familiar individuals. As only a few cells in the STS appear to be sensitive to identity, to suggest a role in individual recognition for all the cells would seem unwarranted. Furthermore, recognition of a head from any view in the horizontal plane can be achieved using four populations of cells, each broadly tuned for one of four views. Although four views (face, both profiles and back) are preferentially encoded, individual STS cells are tuned to many different views (Perrett *et al.* 1989, 1991*a*; Hasselmo *et al.* 1989). It would seem, therefore, that more views are coded than are needed for recognition purposes. What then is the extensive view tuning for?

One hypothesis we are currently investigating is that the STS cells have a role in analysing 'social attention' (Perrett *et al.* 1991*c*). That is, the cells signal the direction of other individuals' attention. A cell responsive to the left profile thus provides a signal that the attention of the observed individual is directed to the viewer's left. This type of information is undoubtedly useful for analysing social interactions between other individuals, such as working out who is threatening whom, and who is soliciting support from whom (Perrett & Mistlin 1990).

(*a*) *Head and gaze direction*

The hypothesis proposed above leads to a different direction of experiments concerning the utility of the cells in social situations. In many cases, the direction in which another person's head is pointing is not a good index of where his or her attention lies. Gaze direction is a much better guide to the focus of another's attention. This leads to several predictions for cell tuning: (i) gaze direction should be important to STS cells; (ii) when cells are tuned to both head view and gaze angle, the optimal direction for the two cues should coincide; and (iii) gaze direction should be more important than head view.

These predictions have been confirmed in recent work and in a re-analysis of previous studies (Perrett *et al.* 1985, 1991*c*). Most (36 out of 56 tested) of the cells sensitive to head view were found to be sensitive to gaze direction (Perrett *et al.* 1985). For all of these cells the preferred gaze direction was compatible with preferred head direction. That is, 18 cells selective for the face view responded more to eye contact than to laterally averted gaze, and 18 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 override sensitivity to head view (see below).

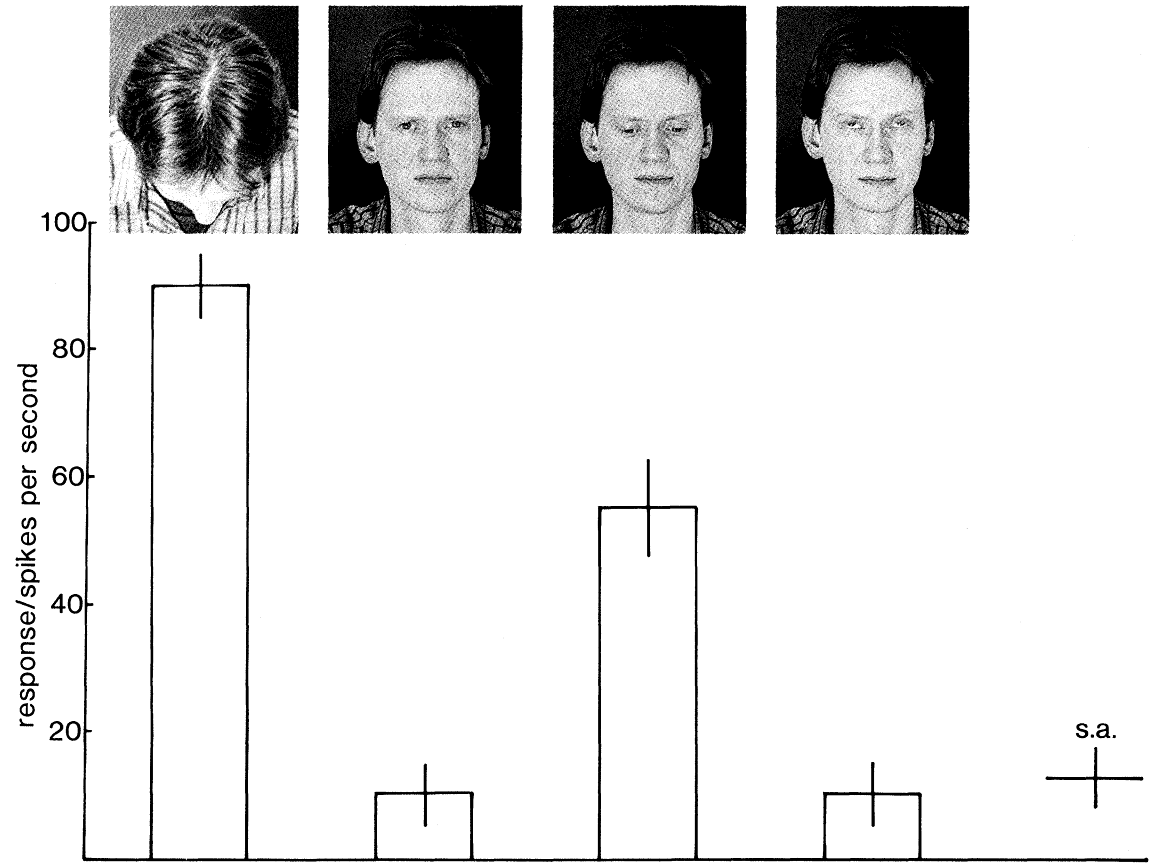

Figure 1. Sensitivity to head and eye gaze direction directed down. Upper: photographic illustration of stimuli used for testing. Lower: mean and standard error of response of one cell to the stimuli. The cell responded well to a view of the head in which the face was rotated towards the ground. With the full face view, the cell responded more when the gaze was directed down than to gaze directed at the viewer (camera) or to gaze averted upwards; s.a., spontaneous activity.

(*b*) *Defaulting to head view sensitivity*

There are circumstances in which the gaze direction is not clear, for example when observing an individual at a distance, or under strong lighting from above which makes the eyebrow ridges cast shadows over the eyes. In these cases, the direction of attention can still be analysed, although with less certainty, from the direction in which the head is pointing. Head angle thus provides a useful 'default' cue. Cells showing combined sensitivity to head view and gaze direction would thus be capable of signalling the direction of attention under a variety of viewing conditions.

(*c*) *Vertical head orientation*

The postulated role in analysing direction of attention also makes sense of the tuning to vertical head posture observed in many cells (Perrett *et al.* 1985; Hasselmo *et al.* 1989). These cells generalize across changes of perspective view in the horizontal plane. Cells coding the raised head responded to the front, profile and back head views when the head was raised. Similarly, cells coding head down generalized across front, side and back head views when the head was lowered. The view tolerance is hard to explain in terms of recognition, but an account based on directed attention naturally extends to cover the generalization. All views of another individual with head raised suggest a focus of attention directed somewhere above the observer's head. Similarly, all views of a head down imply a focus of attention low in the environment.

Figure 1 illustrates sensitivity to head and eye gaze direction directed down. The data support the predictions made above. The cell responded more to the head pointing fully down than to the head level. As the eyes are not visible in the former stimulus, tuning for vertical posture must reflect visual cues derived from the head. Gaze direction was additionally important, as the cells responded to the face view with gaze down but not with gaze level or up. The cell tuning for gaze angle and head view was therefore congruent with a downward orientation being preferred for both. Finally, gaze direction appears to override sensitivity to head direction.

(*d*) *Body posture*

Even when the head cannot be seen, information about the direction of attention can still be obtained from an analysis of the visual appearance of the body. For example, if you see the back of someone's body but their head is occluded from view, it is a 'good bet' that the person's attention is directed away from you.

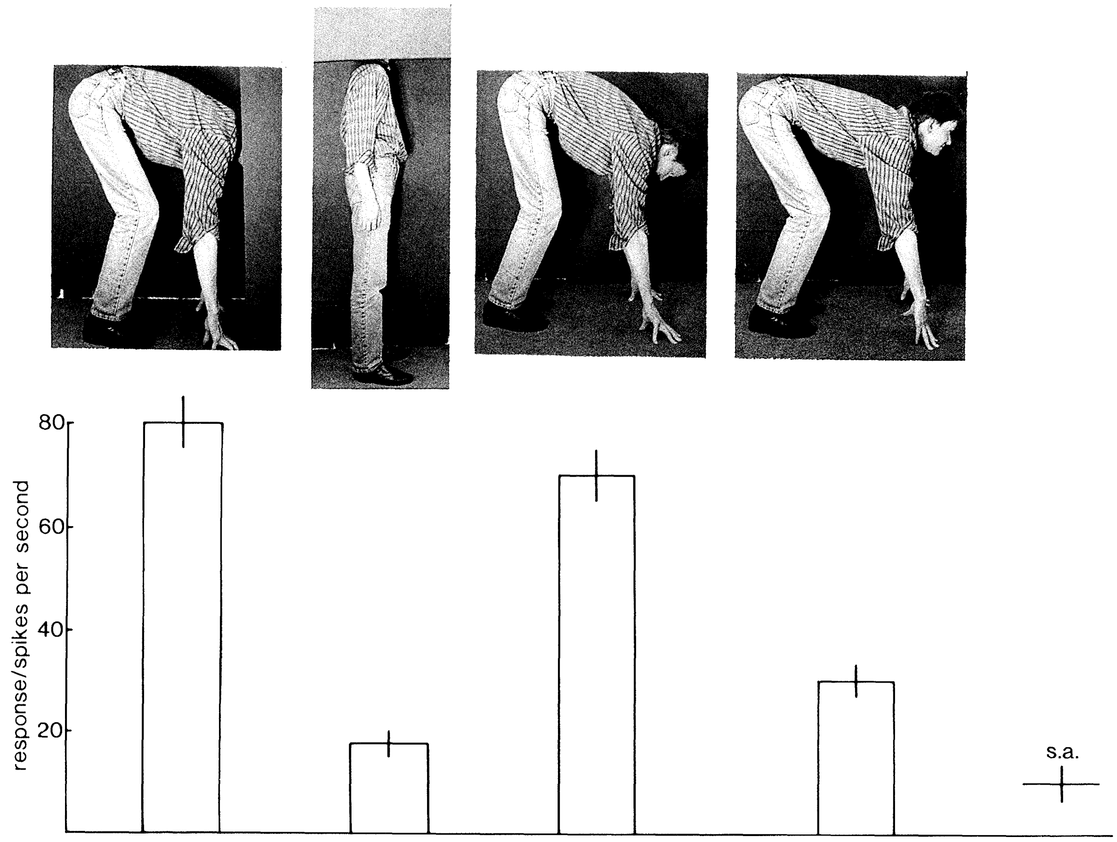

Figure 2. Sensitivity to head and body postures indicative of attention directed down. Upper: photographic illustration of stimuli used for testing. Lower: mean and standard error of response of one cell (also illustrated in figure 1) to the stimuli. With the head covered, the cell responded more to the quadrupedal posture than to the bipedal posture. With the head visible, the cell responded more when the head was pointing at the ground than when it was level, s.a., spontaneous activity.

Certain body postures can act as a cue to the direction of attention in the vertical plane. Macaque monkeys are predominantly quadrupedal but often adopt a bipedal stance when trying to look out over long grass. If one sees a monkey in a bipedal posture then it is likely that the monkey is not attending downwards to the ground but is scanning the horizon. These considerations predict that perhaps human body posture will influence some cells responsive to particular head views.

Figure 2 illustrates responses of the same cell as figure 1, and provides support for this prediction. The notion that the cell was selective for 'attention down' accounts for the sensitivity to body posture. With the head occluded from view, the cell responded more to the quadrupedal posture than to the bipedal posture. As noted above, the quadrupedal body posture is more consistent with attention down than the bipedal posture. Thus the head and body cues were capable of activating the cell independently when presented in isolation. When both the head and body were visible, the head cues took precedence, and head up or head level postures prevented the cell responding to the sight of the quadrupedal body posture.

Figure 3 presents a schematization of possible circuitry by which visual inputs could control activity of an STS cell equivalent to that just described. The cell would be sensitive to three types of visual cue from gaze direction, head posture and body posture. These cues would interact with head cues overriding body cues, and eye cues overriding head cues. The capacity of the 'incorrect' gaze direction to override the 'correct' head view is a product of presynaptic inhibition in the circuit of figure 3, but other synaptic mechanisms are possible. As illustrated, the circuit also accommodates inputs from front, back and profile views, making a total convergence of at least nine sources of visual information. Each of these properties modelled in figure 3 has been observed in the responses of cells such as that illustrated in figures 1 and 2.

It is further possible that information specifying the wrong (bipedal) body posture inhibits directly cells coding attention down. Wiring for this type of input has not been included in figure 3 because it has not yet been confirmed physiologically.

The sensitivity of STS cells to head and eye cues in both the vertical and the horizontal planes thus provides strong support for the postulated role of the area in interpreting the direction of other individuals' attention.

4. ORGANIZATION OF CELLS PROCESSING FACES

Cells responsive to faces have been found in virtually all of the visual sub-regions of the anterior temporal cortex (figure 4). These include the upper bank of the STS (Bruce *et al.* 1981; Perrett *et al.* 1987, 1989, 1991*a*; Harries & Perrett 1991), the fundus of the STS

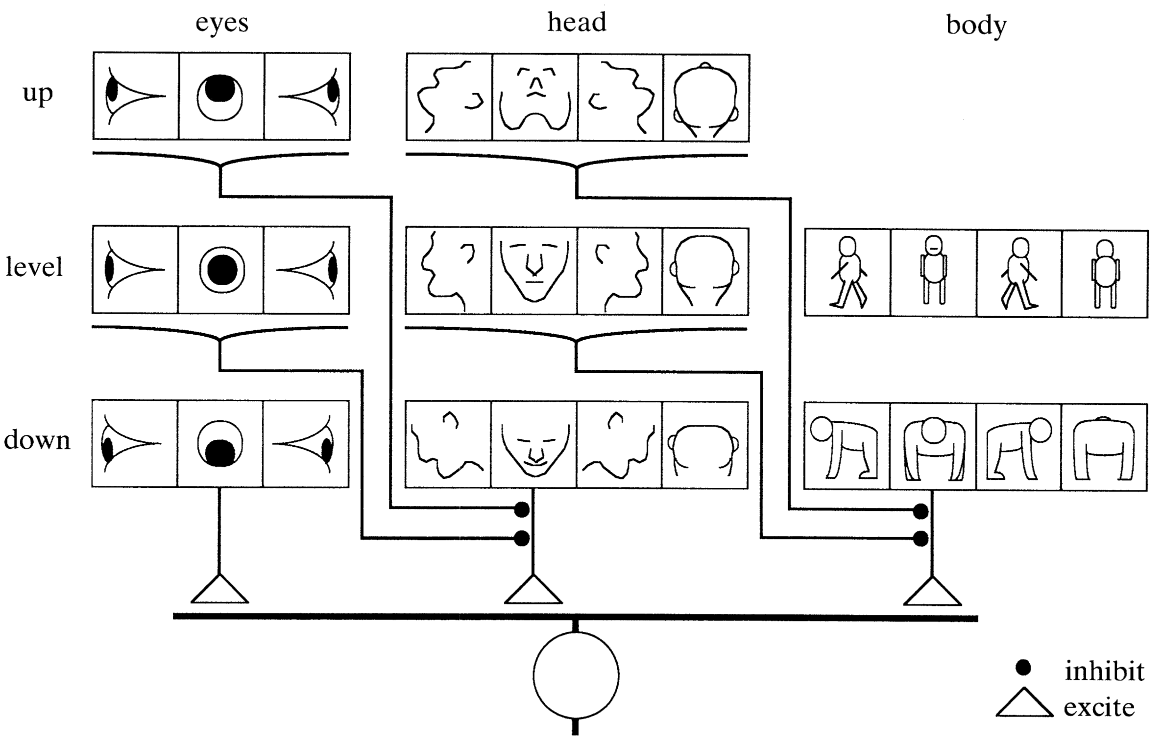

Figure 3. A schematic representation of the connections and types of visual stimuli effecting the responses of an STS cell signalling that another individual's attention is directed down. The diagram shows how very different types of visual input interact through excitatory and inhibitory connections to establish selectivity for a conceptually coherent set of stimuli. The cell (large circle) receives view-specific excitatory inputs from cells selective for the visual appearance of eyes down, head down, and quadrupedal body posture. Gaze directed level or up prevents response to the down cues by presynaptic inhibition (see text for details).

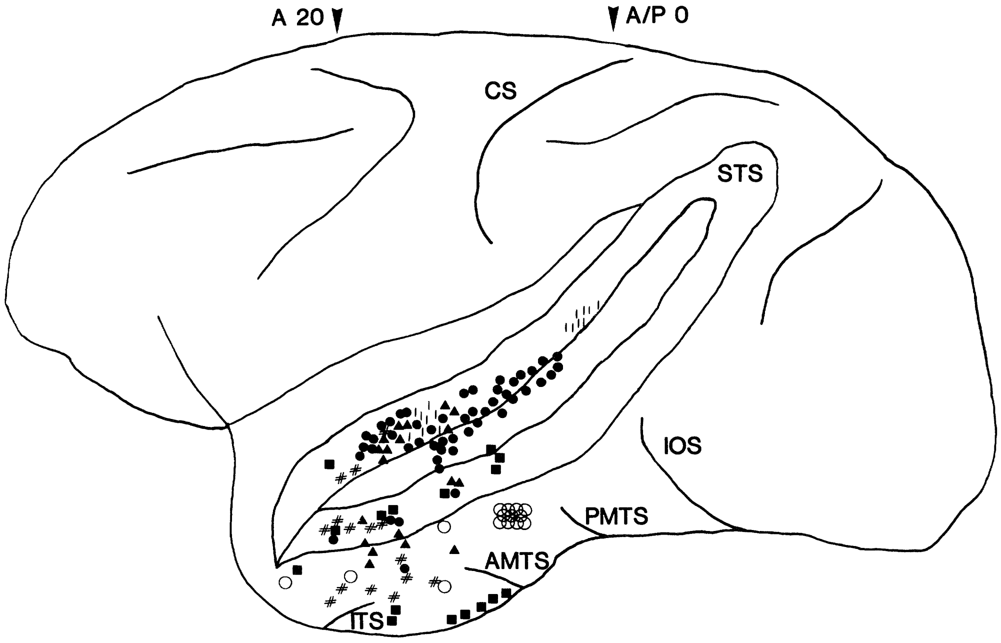

Figure 4. Location of cells in the temporal cortex selective for faces from a selection of studies. Drawing of a left side of a rhesus macaque brain showing major sulci. Abbreviations: STS, superior temporal sulcus; IOS, inferior occipital sulcus; CS, central sulcus; ITS, inferior temporal sulcus; AMTS, anterior medial temporal sulcus; PMTS, posterior medial temporal sulcus. Symbols: ●, Perrett (1982, 1985, 1987); ▲, Rolls (1984); ■, Yamane (1988); #, Hasselmo (1989); |, Harries (1991); ○, Tanaka (1991).

(Perrett *et al.* 1982, 1985), the lower bank of the STS (Rolls 1984; Mikami & Nakamura 1988; Yamane *et al.* 1988) and the lateral and ventral regions of inferior temporal (IT) cortex (Rolls 1984; Yamane *et al.* 1988; Hasselmo *et al.* 1989; Tanaka *et al.* 1991; M. Brown & F. Wilson, personal communication). The density of cells within these cortical areas varies between studies and possibly between hemispheres (Perrett *et al.* 1984, 1988*a*). In the STS, the cells responsive to faces occur in 3–5 mm patches (Harries & Perrett 1991). Grouping of cells with similar physiological properties probably exists throughout the temporal cortex. Such patches may account for the variation in reported frequency of cells between studies.

It is interesting that output connections from the STS also exhibit a modular organization of repeating 3–5 mm patches connected to parietal cortex (Harries & Perrett 1991). These outputs could present a route through which visual cues about social attention can access parietal systems involved in spatial awareness and attention.

Coding of facial information appears to be qualitatively distinct in different regions of the temporal cortex. In the lateral IT, the cells appear to be selective for orientation in the fronto-parallel plane (i.e. different cells responding to upright and horizontal faces; Tanaka *et al.* 1991), whereas those in the STS generalize across orientation (Perrett *et al.* 1982, 1984, 1985, 1988*a*). The connections between cells responsive to faces in the different temporal areas are not known, but the sensitivity to orientation would suggest the STS cells pool outputs from IT cortex. This would be consistent with the anatomical projection from IT into STS (Jones & Powell 1970; Seltzer & Pandya 1978).

The functional properties of cells responsive to faces in the two areas may also differ. Sensitivity to face identity may be more frequent in IT than in the STS (Baylis *et al.* 1985; Perrett *et al.* 1984*a*, 1991*a*; Yamane *et al.* 1988). Sensitivity to gaze direction appears to be common in the macaque STS (60% of the cells responsive to frontal head views), but has not yet been found in IT.

5. RELATION TO PROSOPAGNOSIA

It has been suggested that the cells responsive to faces in the macaque STS are part of a neural system analogous to that to which damage underlies prosopagnosia in man. To verify this link, we designed a gaze direction task for human subjects. As gaze direction was very important for STS cells, patients suffering from prosopagnosia should display reduced capacity to discriminate gaze direction if their disability reflected damage to mechanisms equivalent to those we were studying in the monkey. Work with one patient, R.B., revealed that he was indeed very poor at discriminating gaze direction even though he was excellent at many other tasks requiring fine visual discrimination (Perrett *et al.* 1988*b*).

This finding supported a link between the macaque STS cells processing faces and deficits in the perception of particular facial attributes within prosopagnosia. Far stronger evidence for a link comes from work by Campbell *et al.* (1990) who reported that monkeys with bilateral lesions to the STS were also impaired in the identical gaze task, but were unimpaired or mildly impaired in other visual tasks, a result confirmed by Heywood & Cowey (this symposium). Ablation of the macaque STS would, on this evidence, appear to leave the monkey with at least one feature of some prosopagnosic patients. However, the main characteristic of human prosopagnosia is that patients fail to recognize the identity of faces, and it is therefore surprising that STS ablation in monkeys does not appear to affect the identification of faces (Heywood & Cowey, this symposium). Hence the main damage in prosopagnosia presumably involves brain areas different to the human equivalent of the macaque STS.

The observations that cells process faces over a wide area of temporal cortex means that lesions to restricted parts of the temporal cortex may fail to affect face recognition. Furthermore, the possibility that subregions process faces in different ways means that lesion of the STS may only affect some aspects of face recognition. Indeed, even in human subjects, brain damage can produce a variety of face-processing defects (Young, this symposium). Campbell *et al.* (1990) argue that the sensitivity to eye gaze may be a dissociable condition within patients suffering from face recognition disorders. One patient they tested was unimpaired at the gaze task but was impaired in face recognition. Indeed the deficits may doubly dissociate, as patient R.B. was markedly impaired on the gaze task (Perrett *et al.* 1988*b*) but was mildly impaired in the recognition of famous faces (he recognized 11 of 20 famous faces, whereas the author could recognize 14 out of 20, unpublished observations).

From the widespread distribution of face processing modules it follows that to prevent face recognition in a monkey or human it may be necessary to disrupt all the relevant modules. This might arise after damage to each of the modules, or might follow a disconnection of the flow of information through the system of modules, perhaps by selectively damaging face processing modules early in the processing chain (e.g. lateral temporal cortex).

In conclusion, the neurophysiological studies suggest that face processing is distributed across several different mechanisms within the temporal cortex of monkeys. Likewise, there appear to be several different types of visual deficit associated with prosopagnosia in humans. Cell populations within the STS cortex are heavily involved in the analysis of gaze direction. Study of this aspect of their visual sensitivity offers a potential link to the perceptual losses occurring in some forms of prosopagnosia.

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Discussion

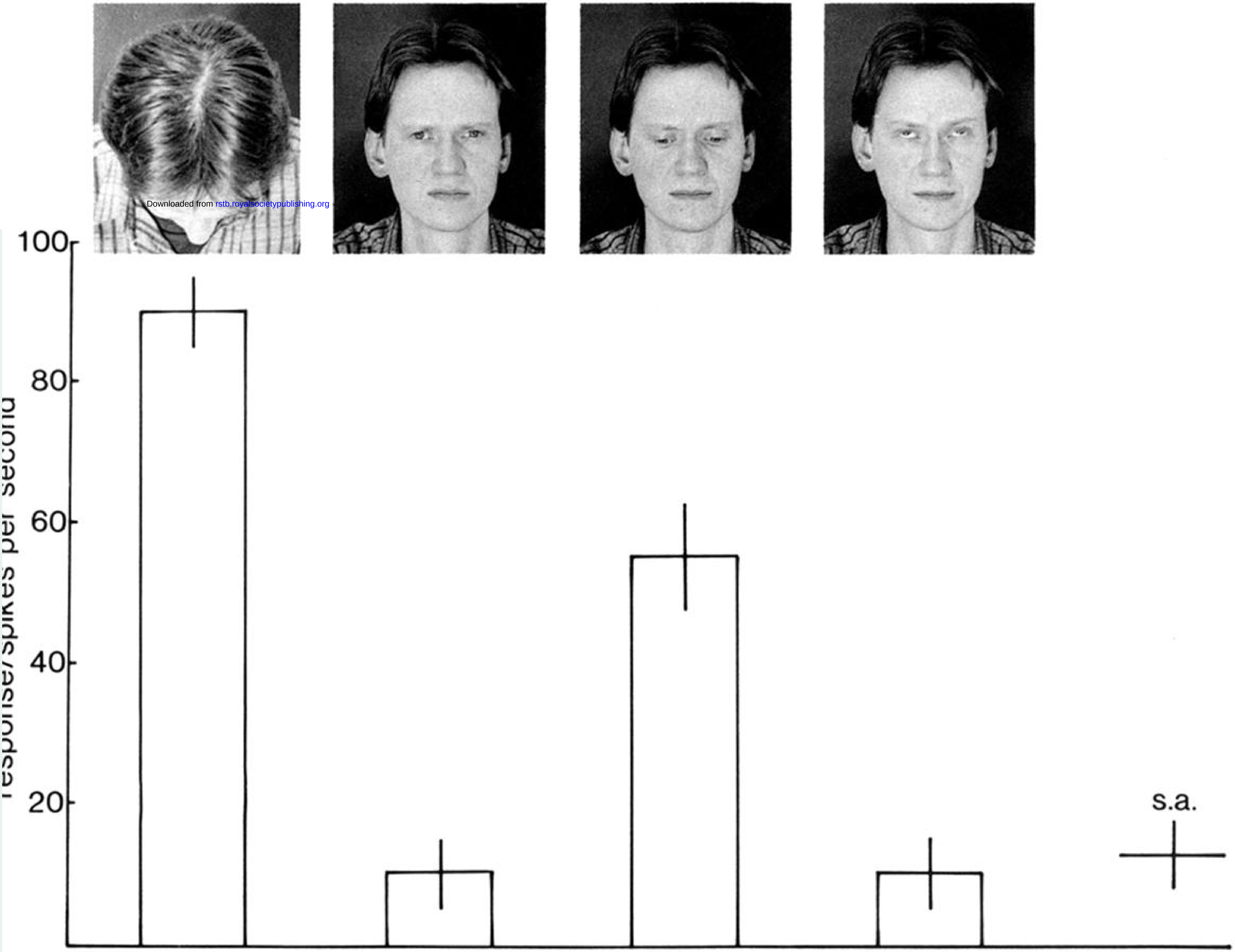
E. T. Rolls (*Department of Experimental Psychology, University of Oxford, U.K.*). In our investigation of the view-dependency of face-selective neurons (Hasselmo *et al.* 1989), we found that, insofar as these neurons had view-dependency (and the fact that they had less than those the authors studied may be because our sample was more anterior), there was very little evidence for a small number of characteristic views. I suggest that this is consistent with the hypothesis that competition helps to build neurons with different responses to each other (see Rolls, this symposium), and would like to ask therefore why the authors postulate that a few characteristic views are represented.

D. I. Perrett. We postulate that a few characteristic views are represented in the higher stages of visual processing because this is consistent with psychological and physiological findings and also theoretical considerations (see Perrett *et al.* 1991*a, b*). The failure of Hasselmo *et al.* to find evidence for characteristic views may be due to several reasons.

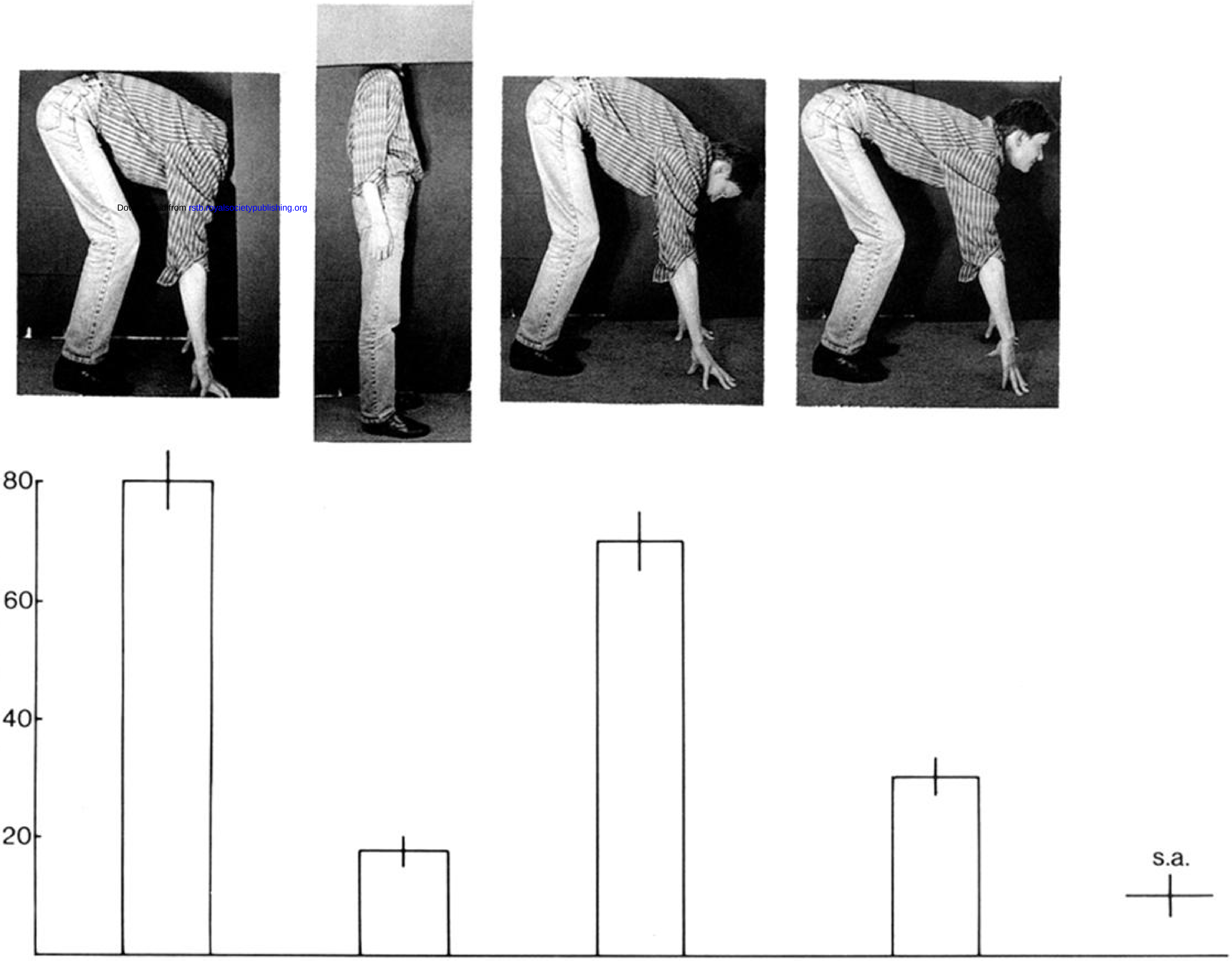
1. Small sample size. They sampled 37 neurons with a full range of views (although 49 lines appear in figure 11, Hasselmo *et al.* 1989). In our study of 73 neurons (tested with a full range of views) we found some evidence for differences across subjects and across regions.

2. Inappropriate methods of analysis. The formula used by Hasselmo *et al.* (1989) to assess the overall orientation specificity can produce erroneous estimates. We found the formula produced poor estimates of optimal angles particularly for cells tuned to two views 180 degrees apart (e.g. left and right profiles) (see Perrett *et al.* (1991*a*) for detailed discussion).

3. Biased view testing. Thirteen of the 28 cells studied with digitized images by Hasselmo *et al.* (1989) were tested with more front views than back views. This bias would miscategorize the tuning of cells for profile or rear views.



gure 1. Sensitivity to head and eye gaze direction directed down. Upper: photographic illustration of stimuli used for sting. Lower: mean and standard error of response of one cell to the stimuli. The cell responded well to a view of the ead in which the face was rotated towards the ground. With the full face view, the cell responded more when the gaze as directed down than to gaze directed at the viewer (camera) or to gaze averted upwards; s.a., spontaneous activity.



gure 2. Sensitivity to head and body postures indicative of attention directed down. Upper: photographic illustration stimuli used for testing. Lower: mean and standard error of response of one cell (also illustrated in figure 1) to the muli. With the head covered, the cell responded more to the quadrupedal posture than to the bipedal posture. With e head visible, the cell responded more when the head was pointing at the ground than when it was level, s.a., ontaneous activity.