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The Role of the `Face-Cell' Area in the Discrimination and Recognition of Faces by Monkeys [and Discussion]

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The role of the 'face-cell' area in the discrimination and recognition of faces by monkeys

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SUMMARY

Cortical neurons that are selectively sensitive to faces, parts of faces and particular facial expressions are concentrated in the banks and floor of the superior temporal sulcus in macaque monkeys. Their existence has prompted suggestions that it is damage to such a region in the human brain that leads to prosopagnosia: the inability to recognize faces or to discriminate between faces. This was tested by removing the face-cell area in a group of monkeys. The animals learned to discriminate between pictures of faces or inanimate objects, to select the odd face from a group, to inspect a face then select the matching face from a pair of faces after a variable delay, to discriminate between novel and familiar faces, and to identify specific faces. Removing the face-cell area produced no or little impairment which in the latter case was not specific for faces. In contrast, several prosopagnosic patients were impaired at several of these tasks. The animals were less able than before to discern the angle of regard in pictures of faces, suggesting that this area of the brain may be concerned with the perception of facial expression and bearing, which are important social signals in primates.

1. INTRODUCTION

The existence of an acquired defect in visual recognition that is selective for faces has always been controversial, although the first reports of visual cortical neurons that were optimally stimulated by complex stimuli such as hands or faces (Gross *et al.* 1969, 1972) undoubtedly revived interest in this possibility. However, it is never a straightforward matter to establish the role in behaviour of particular groups of cells from their receptive field properties. For example, such cells may be primarily concerned with facial discrimination as opposed to recognition, or with facial expression or orientation, or with the autonomic and emotional response to faces.

Not surprisingly, results from single-unit recordings from cells in the temporal lobe of the macaque monkey have remained stubbornly resistant to any interpretation other than that they are specialized for the processing of the facial image (for a review, see Desimone (1991)). Cells that respond preferentially to the visual presentation of a face are located in both the inferior temporal gyrus and the banks and floor of the superior temporal sulcus (STS) but are more prevalent in the latter, in areas TPO and TPm (see figure 1). Furthermore, receptive field properties have been described for cells responding selectively on the basis of facial identity (Baylis *et al.* 1985), expression (Hasselmo *et al.* 1989) and on the basis of head and eye position (Perrett *et al.* 1985). The particular relevance of these more recent findings to an understanding of the clinical condition of prosopagnosia has not gone unnoticed. The latter condition consists of an arguably selective, but nevertheless striking, impairment in the recognition of previously familiar faces following brain damage. In addition, dissociations of impairments in the visual recognition of facial identity and facial expression have been reported (Bruyer *et al.* 1982; Kurucz & Feldmar 1979) and prosopagnosic patients have been reported with gross abnormality in sensitivity to direction of eye gaze (Perrett *et al.* 1988; Campbell *et al.* 1990). Electrophysiological evidence has thus bolstered the view that independent systems for visual recognition exist, each specialized for the processing of particular kinds of visual stimuli. One way of establishing the veracity of the claim that prosopagnosia is the result of damage to the human homologue of cortex in the monkey's STS is to assess the ability of monkeys, following removal of cortex in STS, on tasks on which prosopagnosic patients are impaired. It is the results of such a study which we report. The performance of three animals with bilateral ablation of STS was compared with that of three unoperated controls on tasks of visual discrimination, visual recognition and visual identification of faces and objects. In addition, performance was compared with that of several prosopagnosic patients on identical tasks.

2. METHODS

Subjects and surgery

Six adult male rhesus monkeys (*Macaca mulatta*) were used. They were experimentally naive at the start of training. Following training three animals

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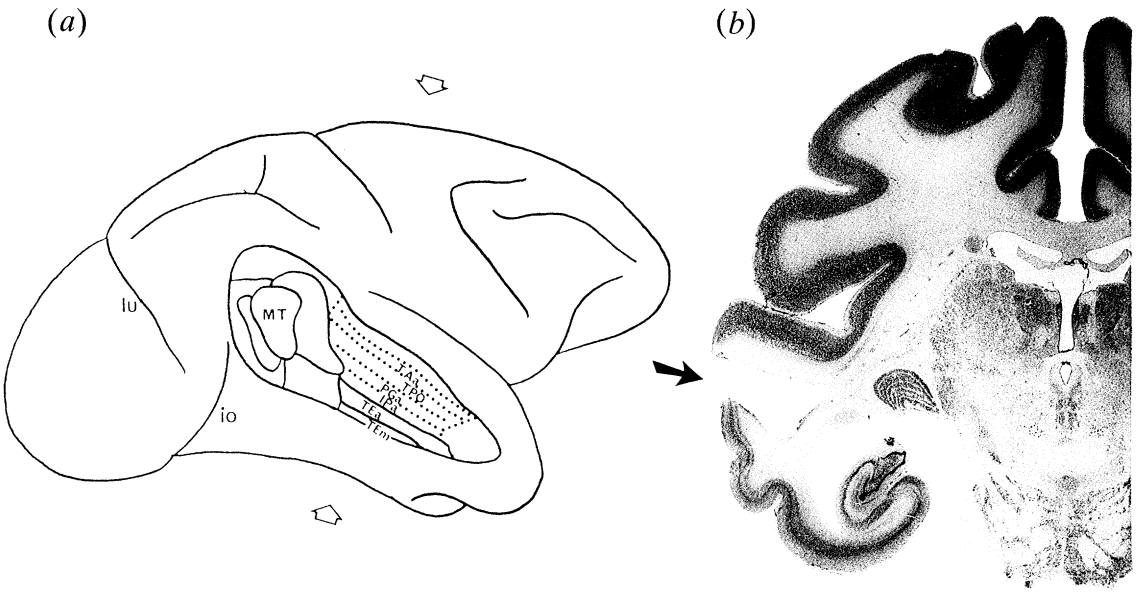

Figure 1. (*a*) Lateral view of the macaque brain showing the superior temporal sulcus, which has been opened out to display the subdivisions proposed by Seltzer & Pandya (1978). Areas TAa, TPO and PGa comprise the superior temporal polysensory area STP. Sulcal abbreviations: lu, lunate sulcus; io, inferior occipital sulcus. (*b*) A photomicrograph of a coronal section through the left hemisphere of the monkey brain. The level of the section is indicated by an arrow in (*a*). The cortex in the superior temporal sulcus, indicated by a black arrow, has been removed by aspiration.

underwent bilateral removal of both banks and the floor of STS, extending anteriorly from 5 mm in front of the inferior occipital sulcus to a point about 5 mm from the temporal pole, a rostro-caudal distance of about 20 mm (figure 1). Cortical ablation was done by aspiration under aseptic conditions and deep general anaesthesia. Surgical details are available elsewhere (Heywood & Cowey 1987).

For the purposes of comparison, four well documented cases of prosopagnosia were tested on identical tasks. These were patients M.S. (Newcombe & Ratcliff 1975), P.H. (Young & De Haan 1988), N.R. (De Haan *et al.* 1991) and A.B. (McConachie 1976).

Apparatus

Visual stimuli were presented on a 20 inch Mitsubishi colour monitor. The screen was controlled by a Pluto II graphics device (Electronic Graphics Ltd.) providing a screen resolution of 768 pixels horizontally by 576 pixels vertically. Frame-grabbed images were displayed on the screen in a maximum of 128 levels of grey. Alphanumeric characters could be displayed where a resolution of eight bits per gun provided the choice of colours from a large palette.

The monkey sat in a wheeled transport cage placed in front of the monitor. He could respond to visual stimuli by reaching out through the bars of the cage to a 'touch screen' placed immediately in front of the monitor and sensitive to the precise position of the animal's hand. The touch-sensitive screen and graphics controller were interfaced with an IBM computer. Correct responses were rewarded with a peanut delivered into a food well positioned centrally below the screen. Ambient illumination in the testing cubicle was provided by light from the monitor at a background screen luminance of 16.0 cd m^{-2}. Animals could be observed by the experimenter from an adjacent room via a video camera and monitor. An identical monitor and touch screen were used for visual displays presented to human observers.

(*a*) *Visual discriminative stimuli*

Twenty-six alphanumeric characters (Hershey characters 3001–3025) were used for the discrimination of form. The characters were drawn with 2.5 mm line widths and had a height × width of no greater than 2 cm × 1 cm. Frame-grabbed images of monkey and human faces and objects were selected from a large library of such images. Each image was adjusted to be of an equivalent size (7 cm × 7 cm) and to contain the full range of grey values.

(*b*) *Nine-choice oddity*

Pretraining

Animals first learned to touch a 10 cm white square that appeared against a grey background at the centre of the screen. The square appeared with an intertrial interval of 5 s and remained on the screen until touched, which resulted in the delivery of a peanut and the disappearance of the square. Animals received 50 trials a day and rapidly learned to respond. The square was then replaced by a white alphanumeric character, the letter 'A', which appeared from trial to trial at random positions on the screen. Animals rapidly transferred to touching this stimulus for a peanut reward. Eight identical characters, which dif-

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fered from the target character, were then introduced onto the screen in random positions with the constraint that no two characters could appear in either the same column or row. The animals were then required to touch the letter 'A' while ignoring the irrelevant items. Touching an irrelevant character resulted in an error being recorded and the extinction of the display. The target remained the same but the character comprising the identical unrewarded stimuli changed in form and colour from trial to trial. The positions of target and non-target stimuli were randomized from trial to trial. Animals received 100 trials a day. The intertrial interval for this and subsequent tasks was 5 s. Within two days all the monkeys achieved an arbitrary criterion of 80% correct responses. For the following two days the target item now changed randomly in colour and form but the unrewarded character remained unchanged from trial to trial. The colours were selected from an arbitrarily selected palette of 256 colours. Again, within two days all animals were scoring more than 80% correct.

(*c*) *Preoperative testing*

Form discrimination

For ten days animals received 100 trials a day where the target and the eight unrewarded stimuli were changed every ten trials although the spatial arrangement of the stimuli was randomized from trial to trial. For the next ten days the task was identical to that just described except that colour differences were removed and the oddity discrimination was based entirely on form differences. Finally, nine-choice oddity performance was tested for 500 trials on a new stimulus set where the problem changed from trial to trial.

(*d*) *Three-choice oddity*

Pretraining

Following nine-choice oddity animals were transferred to a three-choice oddity paradigm. The discriminanda were a set of 16 achromatic faces. On each trial a single face appeared at the centre of the screen and the animal was required to touch it. This resulted in the appearance of two more faces, one on each side of the central stimulus. One face was identical to the central stimulus, the other was the face of a different person. Touching the different face resulted in the delivery of a peanut. One hundred trials were presented a day. On any trial the correct stimulus could appear randomly to the left or right of the central stimulus and the correct and incorrect stimulus were selected randomly from the stimulus set. Training continued until a criterion of 90 correct in a single session was achieved. An identical procedure was used for the discrimination of objects, again using a set of 16 objects. A novel series of faces was then introduced where for a single trial the three stimuli were selected such that each face was of a different view (left and right profiles and head on). However, two faces were of the same person and the third was of a different person. Testing was carried out as described above. On completion of training three animals underwent bilateral removal of STS.

Postoperative testing

Postoperative testing was the same as that described above. In addition, oddity performance was assessed for 1000 trials for sets of novel faces and objects before a further four tasks were presented.

1. Delayed non-matching to sample (DNMTS).

The procedure was identical to that described for oddity discrimination except that a response to the central stimulus (the 'sample) resulted in its disappearance. There was then a delay followed by the presentation of two faces, one identical to the sample and the other a different face (the 'distracter'). The animals were required to touch the 'distracter'. Animals were tested for 1000 trials each for familiar and novel faces and objects, in each case using a set of 16 stimuli. The delay for each trial was selected randomly (either 0, 1, 2, 5, 10, 20 or 40 s).

2. Familiarity judgements.

The 16 faces used for preoperative acquisition and postoperative retention of oddity were used in addition to a set of 16 novel faces. On each trial animals were presented with two faces; one was a familiar face, which was randomly paired with a novel face. Each familiar face appeared once in a block of trials after which the block was repeated with a different random pairing of novel and familiar face. Animals were required to touch the novel face.

3. A task requiring visual identification.

In this task, the four faces A, B, C and D were rewarded by 0, 1, 2 and 4 peanuts, respectively. On each trial two of the four faces were presented on the screen and whichever was touched yielded the appropriate number of peanuts. All possible pairings of faces occurred and on each trial the monkey was expected to select the stimulus with the greater reward value. Testing continued until a criterion of 90% correct was reached.

4. Concurrent learning of faces.

Animals were required to learn a two-choice simultaneous discrimination between monkey faces to a criterion of 90% correct. In a further test, four monkey faces were used, each of which could appear as a left or right profile or face-on, i.e. 12 stimuli altogether. Two of the faces were the rewarded stimuli the other two were unrewarded, regardless of their orientation. A two-choice discrimination was presented where a randomly selected view of either of the positive stimuli was paired with a similarly selected negative stimulus. Testing continued until a criterion of 90% correct in a single session was reached.

5. Discrimination of eye gaze.

The selectivity of some neurons in STS to head and eye position (Perrett *et al.* 1985) and to facial expression (Hasselmo *et al.* 1989) has promoted speculation that STS is a specialized system for the facilitation of social communication (Desimone 1991). Furthermore, Perrett *et al.* (1988) reported an absence of sensitivity to eye gaze in a prosopagnosic patient. In an additional experiment five monkeys were tested for

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their ability to discriminate the direction of eye gaze, pre- and postoperatively. In addition, two prosopagnosic subjects, A.B. and K.D. (Christen *et al.* 1985) were tested in an identical fashion. Full details are published elsewhere (Campbell *et al.* 1990). A single face was photographed in one of three head orientations, 20 degrees to the left or right, or face on. For each head position the eyes could be 5, 10 or 20 degrees to the left or right, or looking directly at the observer. On each trial, animals were presented with a pair of faces, one looking at the monkey, the other with eyes averted. Animals were required to displace the latter to reveal a foodwell baited, when the choice was correct, with food reward. The three rewarded stimuli were each paired in every combination with the 18 unrewarded faces in a single session, where the correct stimulus appeared randomly to the left or right. Head position could not, therefore, determine the correct choice. The measure of performance was the percentage correct at each eye deviation, pre- and postoperatively. Prosopagnosic subjects were asked to indicate the photograph in which the eyes were looking at them.

3. RESULTS†

(*a*) *Animal studies*

Nine-choice Colour and form oddity

The monkeys with STS lesions were indistinguishable from controls in their ability to select the odd-one-out when the latter differed in colour and form (mean % correct, preoperative: unoperated, 79.2; STS, 66.2; postoperative: unoperated, 90.1; STS, 89.0) or form alone (mean % correct, preoperative: unoperated, 66.3; STS, 65.2; postoperative: unoperated, 79.5; STS, 80.3). Both groups showed a comparable improvement on postoperative retention. For each task, there was within-problem learning which did not differ overall between groups and was evident both pre- and postoperatively to the same extent in normal and operated animals.

However, when tested with a novel stimulus set where the stimuli changed from trial to trial the STS group were significantly, but mildly, impaired postoperatively (mean % correct, preoperative: unoperated, 85.7; STS, 87.2; postoperative: unoperated, 87.1; STS, 80.7).

Three-choice face and object oddity

Animals with STS lesions were mildly, but not significantly impaired when compared with unoperated controls for 1000 trials each of face and object discriminations postoperatively. There was no overall difference in the scores for objects and faces (mean % correct for faces and objects respectively: unoperated, 77.3 and 76.8; STS, 72.8 and 69.5). However, although both groups eventually scored better on faces they initially found faces more difficult. The operated group was not differentially impaired at either objects or faces. Nevertheless, while the performance of both groups improved across days, the operated animals were impaired during the early postoperative sessions but reached a normal level of performance, i.e. they would have shown a significant group difference if errors to criterion had been measured. However, this was true for both objects and faces.

The results for oddity performance and unfamiliar faces and objects are essentially the same as above. Overall, STS animals performed more poorly than unoperated controls but not significantly so (mean % correct for faces and objects respectively: unoperated, 87.9 and 87.8; STS, 80.4 and 82.1). Neither was there any significant interaction with type of stimulus material or days of testing. When a new set of faces from E. K. Warrington's Face Recognition Test were used and animals were tested to a criterion of 90% correct, STS animals were significantly impaired (mean errors: STS, 263; unoperated, 65).

The overall results indicate a mild impairment in form discrimination following STS lesions which is not specific to faces.

When animals were required to select the odd-one-out where the faces were presented at different views within a trial (left profile, right profile and face-on) and the combinations were selected randomly from trial to trial, there were no significant group differences. This was true not only for postoperative retention of material seen preoperatively (mean % correct: unoperated, 75.3; STS, 77.0), but also for the acquisition of new material (mean % correct: unoperated, 78.9; STS, 72.9). The results were essentially the same whether monkeys were required to discriminate human or simian faces.

Delayed non-matching to sample

STS lesions did not affect the ability to perform delayed non-matching to sample with faces or objects at any of the delays. Performance was better for novel stimuli, significantly so for objects over all delays and for unfamiliar faces at longer delays, presumably reflecting a greater ease in making familiarity judgements between the sample and distracter rather than a relative recency judgement in the case of familiar stimuli. Thus animals with STS lesions show no recognition memory impairment in a task requiring the integrity of short term visual memory. Figure 2 summarizes the results.

Familiar and unfamiliar judgements

When monkeys were required to select the unfamiliar face in a two-choice discrimination between a familiar face selected from a set of 16 and an unfamiliar face selected from a set of the same size, there were no group differences in performance either in trials to reach a criterion of 90% correct (mean: unoperated, 736; STS, 1184) or in percentage correct for trials where each unfamiliar face appeared for the first time. Therefore, in addition to making recency judgements (delayed matching to sample), STS animals were unimpaired at discriminating highly familiar from unfamiliar faces.

† Results were analysed by using analyses of variance. Significant results are reported at the 5% significance level. Detailed statistics are available from the authors.

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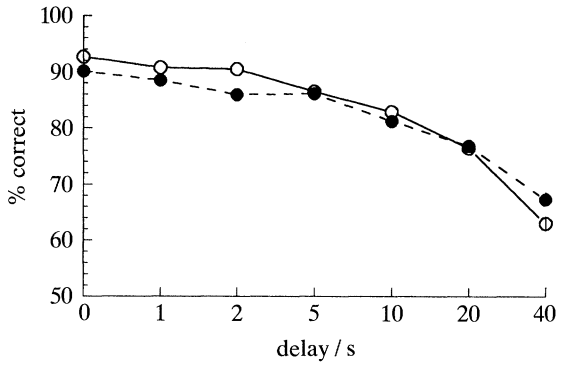

Figure 2. Mean percentage correct for unoperated (open circles) and STS (closed circles) group for delayed non-matching to sample where each point is the group mean of scores on novel and familiar faces and objects. Groups did not differ significantly in their performance on each of the tasks.

Identity task

Although animals with STS lesions are mildly impaired at object and face discrimination and unimpaired at making recency and familarity judgements, none of these tasks required animals to identify a stimulus. A deficit in the identification of a visual stimulus would presumably lead to an impairment on a task where animals are required to learn to associate each of four different faces with different reward values, where reward value represents the identity, or name, of each face. The task proved to be difficult and only two animals in each group learned the appropriate rule. The remaining two, while responding consistently, chose 'B' when confronted with 'B' versus 'C'. This remained true after 2000 trials. However, the two animals that learned the task in each group did not differ in the number of trials taken to reach a criterion of 90% correct on each trial type (unoperated, 664; STS, 432 trials).

Two-choice face discriminations

Animals with STS lesions did not differ from unoperated animals in the number of errors to reach criterion on two-choice face discriminations of novel monkey or human face discriminations. This was also true for concurrent face discriminations where the stimuli were three different views of each of two monkeys and on each trial a view of one monkey was randomly paired with the same, or a different view of another monkey (mean errors: STS, 99; unoperated, 76).

Discrimination of eye gaze

The results are illustrated in figure 3. Monkeys with STS lesions were significantly impaired in the discrimination of eye gaze postoperatively. Although performance improved at increasing angular deviation of the eyes, bilateral removal of STS significantly affected performance at all deviations. There was no evidence that head position was used as a cue in the animals' choice of discriminanda.

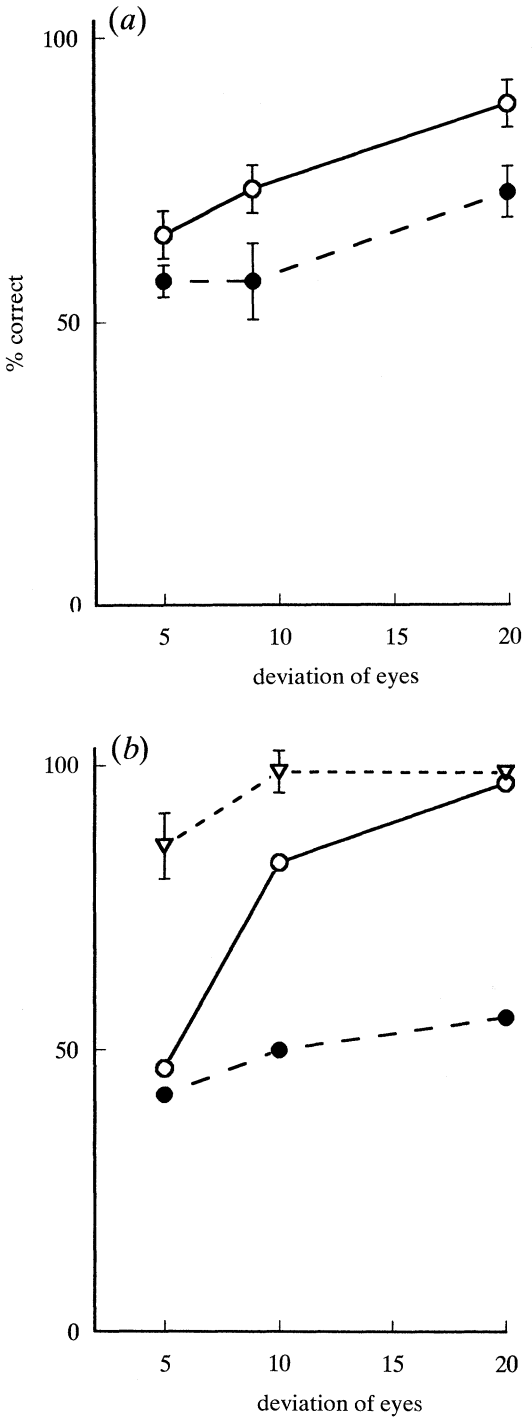

Figure 3. (*a*) Mean percentage correct for 5 monkeys, before (open circles) and after (closed circles) removing the superior temporal 'face-cell' area, on a task of discriminating eye gaze in photographs of faces. (*b*) The performance of two prosopagnosic human subjects (K.D., open circles; A.B., closed circles) and normal human observers (triangles) on the same task. Data redrawn from Campbell *et al.* (1990).

(*b*) *Studies with patients*

Prosopagnosic subjects M.S., A.B., N.R. and P.H. were tested on oddity for faces, familiar and unfamiliar judgements, delayed non-matching to sample and the task of facial identification. Results are presented

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Table 1. *Percentage correct on each of the six tasks presented to each of the four prosopagnosic subjects. Scores for delayed non-matching to sample (DNMTS) are scores summed across delays. Subjects performed almost errorlessly at zero seconds delay and, in the case of M.S. and N.R., fell to close to chance performance at 40 s delay*

	M.S. (%)	A.B. (%)	N.R. (%)	P.H. (%)
face oddity[a]	89	100	99	99
face oddity[b]	59	93	89	92
novel/familiar	53	61	76	69
DNMTS	62	96	68	98
identity, colours	39	89	89	85
identity, faces	54	89	39	62

[a] Faces presented in the same view.
[b] Faces each presented in a different view.

in table 1. The prosopagnosic subjects not only committed errors, particularly when asked to match across different facial views, but response latencies were substantially, and often grossly, longer than those of normal observers whose performance is errorless for the face oddity tasks. Impairments were apparent in judgements of familiarity in all subjects and delayed non-matching was performed poorly by two subjects, M.S. and N.R. The task of learning reward associations as a measure of correct identification was adapted for use in human subjects. Each of the four faces was paired with either 0, 1, 2 or 4 presentations of a brief tone. Subjects were required to maximize the total number of tones produced in a session, by selecting the stimulus that would yield the greater number of tones when presented with a pair of discriminanda. Each session contained 48 trials and subjects completed four sessions, two with different sets of faces and two with two sets of highly discriminable colours. In the case of M.S., whose colour vision was grossly defective, series of achromatic stimuli were used. The results indicate that two of the four subjects (P.H. and N.R.) were substantially worse with faces than with colours. The deficit was not a concomitant of poor performance in the delayed non-matching task, at which P.H. performed normally.

In summary, prosopagnosic subjects showed a range of deficits on identical tasks given to monkeys with bilateral STS removal where impairments were not apparent.

Finally, the results for subjects K.D. and A.B. on a task requiring the discrimination of eye gaze are presented in figure 3. Both subjects showed a significant impairment which was particularly conspicuous in A.B. who responded consistently on the basis of head orientation.

4. DISCUSSION

The complete bilateral removal of the neocortical area in which so-called face cells are common produced only a mild defect in a number of tasks involving the discrimination of faces. Moreover, when a mild disorder was present it was not specific for faces. Although the latter may not be important, given that prosopagnosic patients commonly show various degrees of difficulty in recognizing other objects, there was little evidence that the monkeys had either apperceptive or associative agnosia for faces. In apperceptive agnosia there is a defect in discriminating between similar objects; there was no indication that the monkeys had any great difficulty in discriminating between pictures of faces, even when the faces were presented from different points of view. In associative visual agnosia discrimination is typically spared but recognition of familiarity or identity is grossly impaired; they were not impaired in the experimental monkeys despite the fact that even normal monkeys found the tasks difficult.

Should we be surprised by these results? At least one feature of human prosopagnosia has always contrasted uneasily with the idea that the clinical disorder is caused by the destruction of an area comparable to the cortex in the superior temporal sulcus of the macaque monkey, namely the location of the brain damage. Although there is no reason to expect that comparable cytoarchitectural regions in man and monkey will always be in the same absolute position in the brain, their relative positions show much less variation. Strange then that the focus of the damage leading to associative agnosia involving faces is ventromedial, involving cortex at the extreme medial aspect and including the extensive area 37, which is small or absent in monkeys, and even encroaching on the parahippocampal gyrus and adjacent limbic structures (for recent review see Damasio *et al.* (1990)). The area in which face cells are abundant in monkeys is close to the opposite border of the temporal lobe, adjacent to auditory cortex. It is closer in relative position to the focus of the damage in apperceptive agnosia but the cytoarchitectonic regions involved in the latter do not coincide with those of the cortex in the superior temporal sulcus of macaque monkeys. What then is the function of the processing carried out in the cortex of the superior temporal sulcus? Cells here are tuned to facial features such as where the eyes are looking, whether the mouth is threatening and whether the head is facing towards the viewer, as well as to much less well documented stimuli like hands and bodily movements. These are all informative and important biological social stimuli for primates and it is not uninteresting that the one clear impairment we have found in experimental monkeys was their inability properly to discriminate the direction of gaze (Campbell *et al.* 1990). Such an impairment has been reported in some patients. However, these results should be treated with caution for it is not clear at present whether a pattern discrimination deficit can account for impairments in the discrimination of eye gaze by making it difficult to discriminate small differences in details of the eyes.

The mild pattern discrimination deficit in monkeys is not unexpected. Areas TEa and TEm, on the lower bank of STS are considered to be part of the inferotemporal cortical area, removal of which results in pronounced deficits in discrimination learning bearing

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close similarities to the human agnosic syndrome. It is therefore possible that the discrimination deficits reported here are the result of encroaching into the lower bank of STS and producing the expected consequences of a small lesion to area TE. However, in one respect the impairment in visual discrimination learning following STS lesions does not parallel those expected after small lesions to area TE. Lesions here result in a severe visual discrimination impairment using a wide range of visual stimuli, but the deficit is strangely absent if the discriminanda are rotated versions of one another (e.g. < and >; Gross 1978). However, following lesions to STS, animals are mildly impaired on a range of visual discriminations, including the rotated stimuli discriminations that are spared after TE lesions (Eacott *et al.* 1992). This suggests that the discrimination impairment which follows lesions of STS is not simply the result of associated damage to area TE.

If indeed the impairments in eye gaze discrimination are not a secondary consequence of a pattern discrimination deficit per se then this would be consistent with the proposal that STS is specialized for the processing of biologically important social stimuli. Further experiments on their ability to perceive static and dynamic facial expression might yet reveal the role of this enigmatic area. Meanwhile, the region that corresponds both anatomically and functionally to the medial temporal cortex in the human brain is still unknown. As already mentioned neurons sensitive to facial identity are present in the ventral part of the inferior temporal neocortex (Baylis *et al.* 1985). However, they are intermingled with neurons tuned to non-facial stimuli and the effects of removing this region on visual pattern discrimination learning and retention are so severe that they are almost bound to affect facial recognition. But is prosopagnosia ever truly specific for faces? Most prosopagnosic patients are also agnosic for visually perceived objects, and even when the impairment seems more specific it can be shown with other visual categories, e.g. flowers, dogs, cars. The search for an area of the brain entirely devoted to facial perception and memory and for recognition deficits specific to faces may be no more successful than the hunt for the Holy Grail.

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Discussion

E. T. Rolls (*Department of Experimental Psychology, University of Oxford, U.K.*). There is evidence that, although neurons that respond selectively to faces form approximately 20% of the neurons that respond to visual stimuli in some areas within and on the ventral lip of the macaque superior temporal sulcus (TPO, TEa and TEm), nevertheless there are considerable numbers of such cells in the inferior tem-

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poral visual cortex (e.g. areas TE3 and TE2), where they comprise approximately 5–10% of the neurons that respond to stationary stimuli (Baylis *et al.* 1987). It might therefore be that considerable deficits in face recognition might not be expected unless the lesion was extended to include the TE areas on the inferior temporal gyrus. Further evidence suggesting the importance of the TE areas in processing related to face identity is that cells which reflect the identity of a face are more likely to be found in the TE areas, whereas cells related to face expression are more likely to be found in the cortex in the superior temporal sulcus (Hasselmo *et al.* 1989). Indeed, in view of the results of Hasselmo *et al.* (1989), and the results described by Dr Perrett and Dr Rolls at this meeting, it might be suggested that the cortex in the superior temporal sulcus, especially when relatively posterior, is more involved in face expression and gesture (including head and eye position and movements, and requiring view-dependent representations), whereas the more ventral TE areas in the inferior temporal gyrus, especially relatively anterior, are more involved in face recognition, for which, as Rolls noted, view-independent representations are particularly useful. For these reasons, would it perhaps be appropriate to consider with brain lesions the functions of the, more ventral, TE areas in face recognition and face identity decoding?

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A. Cowey. As we mentioned in the Discussion, impairments in the recognition of the identity of faces might well occur in monkeys after damage to ventral portions of area TE, where neurons sensitive to the identity of a face have been reported. We also mention that more ventral and ventromedial regions of the macaque monkeys brain may correspond to the cortex on the fusiform gyrus of the human brain. It is damage to the latter and to adjacent cortex that has frequently been correlated with a disorder of the recognition of the identity of faces. Unfortunately, the removal of area TE is unlikely to tell us anything that we do not already know. This ablation produces a wide ranging disorder of visual form discrimination and retention and is therefore bound to affect the discrimination and recognition of faces along with other classes of visual stimuli. From what we already know it could not produce a disorder that is restricted to the recognition of faces.

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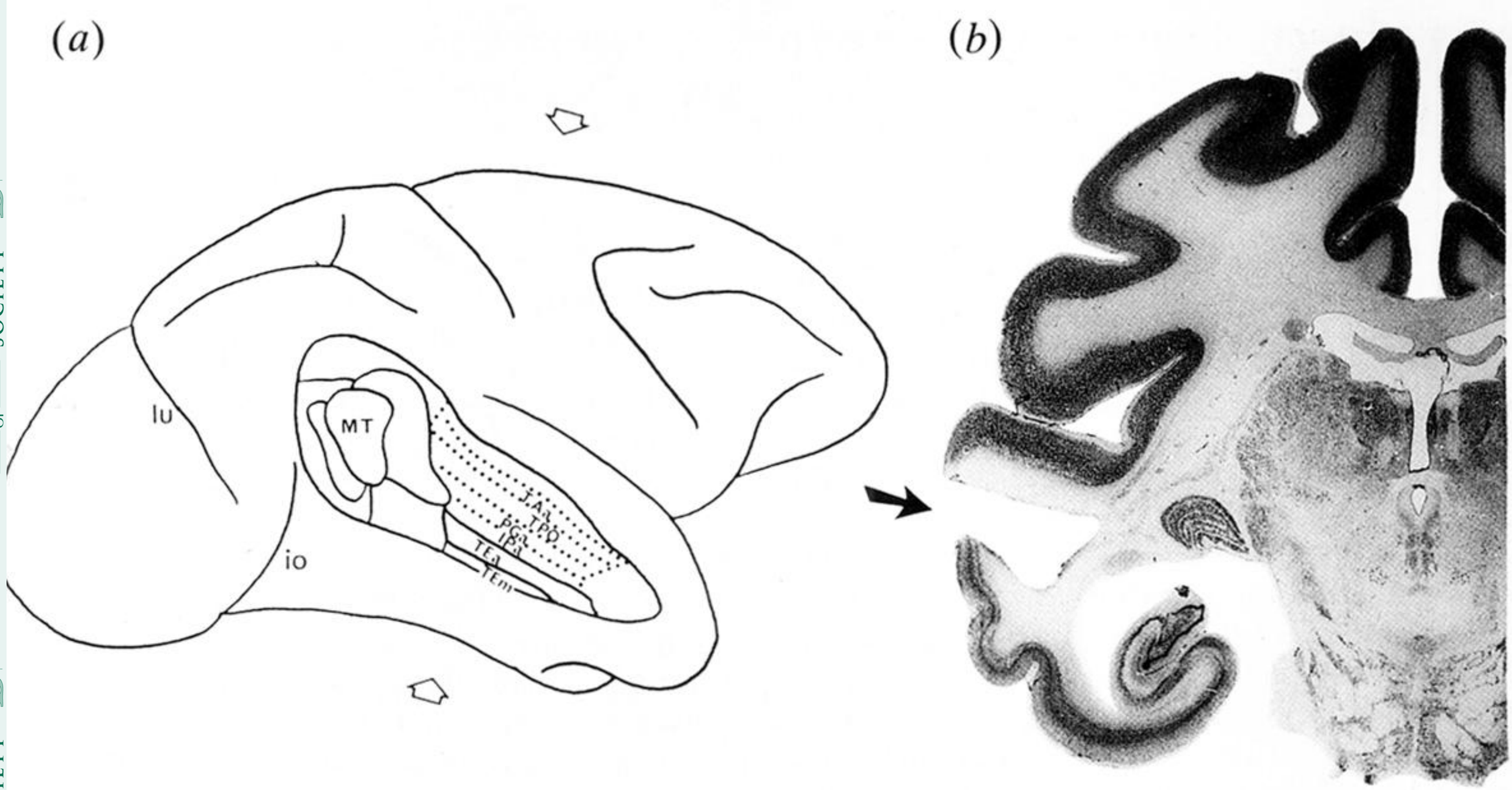

gure 1. (*a*) Lateral view of the macaque brain showing the superior temporal sulcus, which has been opened out to splay the subdivisions proposed by Seltzer & Pandya (1978). Areas TAa, TPO and PGa comprise the superior mporal polysensory area STP. Sulcal abbreviations: lu, lunate sulcus; io, inferior occipital sulcus. (*b*) A iotomicrograph of a coronal section through the left hemisphere of the monkey brain. The level of the section is dicated by an arrow in (*a*). The cortex in the superior temporal sulcus, indicated by a black arrow, has been removed aspiration.