IS FACE RECOGNITION NOT SO UNIQUE AFTER ALL?

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In monkeys, a number of different neocortical as well as limbic structures have cell populations that respond preferentially to face stimuli. Face selectivity is also differentiated within itself: Cells in the inferior temporal and prefrontal cortex tend to respond to facial identity, others in the upper bank of the superior temporal sulcus to gaze directions, and yet another population in the amygdala to facial expression. The great majority of these cells are sensitive to the entire configuration of a face. Changing the spatial arrangement of the facial features greatly diminishes the neurons' response. It would appear, then, that an entire neural network for faces exists which contains units highly selective to complex configurations and that respond to different aspects of the object "face." Given the vital importance of face recognition in primates, this may not come as a surprise. But are faces the only objects represented in this way? Behavioural work in humans suggests that nonface objects may be processed like faces if subjects are required to discriminate between visually similar exemplars and acquire sufficient expertise in doing so. Recent neuroimaging studies in humans indicate that level of categorisation and expertise interact to produce the specialisation for faces in the middle fusiform gyrus. Here we discuss some new evidence in the monkey suggesting that any arbitrary homogeneous class of artificial objects—which the animal has to individually learn, remember, and recognise again and again from among a large number of distractors sharing a number of common features with the target—can induce configurational selectivity in the response of neurons in the visual system. For all of the animals tested, the neurons from which we recorded were located in the anterior inferotemporal cortex. However, as we have only recorded from the posterior and anterior ventrolateral temporal lobe, other cells with a similar selectivity for the same objects may also exist in areas of the medial temporal lobe or in the limbic structures of the same "expert" monkeys. It seems that the encoding scheme used for faces may also be employed for other classes with similar properties. Thus, regarding their neural encoding, faces are not "special" but rather the "default special" class in the primate recognition system.

INTRODUCTION

The current debate on whether faces are "special" or not (Farah, 1996; Tovée, 1998) is firmly rooted in research on humans. The evidence that face recognition in humans may be qualitatively different from the recognition of other objects comes from brain lesion studies (e.g. Farah, Levinson, & Klein, 1995a; Moscovitch, Winocur, & Behrmann, 1997; Yin, 1969), behavioural studies (e.g. Farah, Wilson, Drain, & Tanaka, 1998; Young, Hellawell, & Hay, 1987) and neuroimaging studies (Clark et al.,

1996; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Ohta, & MacDonald, 1992; Sergent & Signoret, 1992). In parallel, we have known of the existence of "face cells" in the monkey brain for many years (Gross, Bender, & Rocha-Miranda 1969). Monkeys' face-recognition performance is remarkably similar to that of humans (Bruce, 1982; Hamilton & Vermeire, 1983; Lutz, Lockard, Gunderson, & Grant, 1998; Mendelson, Haith, & Goldman-Rakic, 1982; Nahm, Perret, Amaral, & Albright 1997; Rosenfield & Van Hoesen, 1979; Wright & Roberts, 1996). It is not surprising, therefore, that a great deal of neural tissue is devoted to the processing of facial information in this species, too. However, perhaps because the techniques are so different, evidence from the animal and human literatures is not fully integrated. The physiological evidence from animal research may considerably enrich the debate and offer information that is lacking in humans because of technical and ethical constraints. On the other hand, the monkey and human work may be difficult to compare because of large methodological differences. Here we briefly review the issues that are most debated regarding the possibility of face-specific mechanisms in humans and we consider relevant evidence from some recent neurophysiological work in the monkey.

During the last 15 years, the interpretation of virtually every piece of evidence for a face-specific system in humans has been contested. Newborns show a preference for facelike patterns (Johnson & Morton, 1991; Valenza, Simion, Macchi Cassia, & Umilta, 1996): However, this preference appears to depend on a crude subcortical mechanism termed CONSPEC, whereas cortical circuits specialised for identifying faces (CONLERN) and responsible for adult-like face recognition are thought to arise at around 2 months of age, presumably through repeated exposure to faces (Morton & Johnson, 1991; Simion, Valenza, Umilta, & Dalla Barba, 1998). A stronger inversion effect was found for faces (i.e., face recognition is more dramatically impaired by inversion than the recognition of other objects, Yin, 1969) but this effect was replicated with dog experts (Diamond & Carey, 1986) and later on with handwriting experts (Bruyer & Crispeels, 1992). Faces seemed to be processed in a more configural (or "holistic") manner than other objects (Farah, 1996; Farah et al., 1995b; Young et al., 1987) but these configural effects have now been replicated with subjects trained to expertise with novel objects (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). Patients with a selective deficit for faces (prosopagnosia; Bodamer, 1947) have been reported (De Renzi, 1986; Farah et al., 1995a), but recent evidence suggests that past studies have failed to control adequately for the dramatic impairment shown by such patients in the discrimination of visually similar nonface objects (Gauthier, Behrmann, & Tarr, 1999b; see also Damasio, Damasio, & Van Hoesen, 1982). A prosopagnosic patient was found to be significantly better with inverted faces than upright faces, contrary to the inversion effect obtained with normal control subjects (Farah et al., 1995a). This was interpreted as evidence for a face-specific recognition module until another prosopagnosic patient (de Gelder, Bachoud-Levi, & Degos, 1998) showed the same "reversed" inversion effect for…shoes! In neuroimaging, the existence of a cortical area that responds preferentially to faces in the right fusiform gyrus has been well established (Kanwisher et al., 1997; McCarthy et al., 1997; Sergent & Signoret, 1992). Recent studies (Gauthier & Tarr, 1997; Gauthier et al., this issue) indicate that the same area can be activated for nonface objects when they are processed at a specific (or subordinate) level (e.g. *Honda* rather than *car*) and that relatively short-term expertise with novel objects can also recruit the "face area" (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999a).

The question of a special status for faces is complicated by the fact that "special" does not mean the same thing for everybody. Hay and Young (1982) dissociated two different aspects of this question: first, the possibility of a specific part of the brain processing faces (specificity), and second, the issue of whether or not faces are recognised in a qualitatively different way (uniqueness). We will consider how neurophysiological evidence in monkeys may

inform the debate on each of these issues. First, however, we offer a summary of the anatomy of face recognition in the monkey and discuss the response properties of face cells in different cortical areas (for more details, see Logothetis & Sheinberg, 1996; or Logothetis, 1998).

THE ANATOMY OF THE FACE RECOGNITION SYSTEM IN THE MONKEY

The cortical pathway that originates in the primary visual cortex and stretches through the extrastriate areas V2 and V4 to the temporal cortices is known to be involved in pattern perception and recognition. In this pathway, the hierarchically highest association area that is exclusively visual is the inferior temporal cortex (IT).

Based on cytoarchitectonic criteria (Von Bonin & Bailey, 1947) and later also on the deficits that follow focal lesions (Iwai & Mishkin, 1969), IT was initially subdivided into a posterior (TEO) and anterior (TE) part. On the basis of both cytoarchitectonic and myeloarchitectonic criteria and of afferent cortical connections, the area TE was later subdivided further into five more or less parallel, rostrocaudally oriented cortical sectors termed areas TE1, TE2, TE3, TEm, and TEa (Seltzer & Pandya, 1978). Input to the area TE comes primarily from the area TEO (Desimone, Fleming, & Gross, 1980; Distler, Boussaoud, Desimone, & Ungerleider, 1993; Shiwa, 1987; Webster, Ungerleider, & Bachevalier, 1991), but also directly from V4 (Shiwa, 1987). Areas TE and TEO possess many other sparser inputs, send feedback projections to other visual areas and medial temporal lobe structures, and project to areas in prefrontal cortex, the limbic system, and to a large number of subcortical structures (see Logothetis, 1998).

Not surprisingly, many of the TE and TEO subdivisions contain cells that have different physiological properties. The area TEO has a coarse visuotopic organisation. Its receptive fields are larger than those of the neurons in area V4

(Boussaoud, Desimone, & Ungerleider, 1991). The cells here respond to moderately complex patterns (K. Tanaka, 1996). The areas TEa, TEm, and TE1-3 are primarily visual and can be activated by stationary stimuli of various complexity (Baylis, Rolls, & Leonard, 1987). Areas in the anterior-dorsal part of STS show sensitivity to motion, whereas cells in the areas TPO, PGa, and IPa are multimodal.

Face cells were discovered by Charles Gross at the beginning of the 1970s (Gross et al., 1969; Gross, Roche-Miranda, & Bender, 1972). In their seminal studies the authors reported a few cells that responded best to complex shapes, such as hands, trees, and human and monkey faces, providing the first evidence for a neurophysiological correlate for Konorski's gnostic (Konorski, 1967). A large number of investigations confirmed and extended these initial findings. Face neurons have been found mainly in the inferotemporal areas TEa and TEm (lower bank of the STS—within an area also called IT) as well as in areas TPO1 and TPO2 (upper bank of the STS—also called superior temporal sensory area or STP) (Baylis et al., 1987; Desimone, Albright, Gross, & Bruce, 1984). Face cells tend to cluster in small patches of 0.5 to 2.5mm across. Face selective cells were also found outside of the STS in the amygdala (Rolls, 1992), the ventral striatum, which receives a projection from the amygdala (Williams, Rolls, Leonard, & Stern 1993), and the inferior convexity of the prefrontal cortex (Wilson, Ó Scalaidhe, & Goldman-Rakic, 1993; Ó Scalaidhe, Wilson, & Goldman-Rakic, 1997).

RELATION TO THE ANATOMY OF FACE RECOGNITION IN MAN

The presence of face cells in several parts of the monkey brain may appear inconsistent with the predominant story in the human of a single "face area" in the right fusiform gyrus (Kanwisher et al., 1997; McCarthy et al., 1997). However, cortical responses to faces in humans are not limited to the right fusiform gyrus. In PET studies, several

regions have been implicated in face processing, in areas of the occipital, temporal, and frontal lobes, although the control conditions in many of these studies make it difficult to know whether the responses are highly selective to faces (see Ungerleider, 1995, for a review). In fMRI studies of face recognition, the fusiform "face area" is often identified using a functional definition (Gauthier et al., this issue; Kanwisher et al., 1997; McCarthy et al., 1997). In such a design, a comparison of passive viewing for faces vs. nonface objects is used by experimenters to define in each subject the part of the fusiform gyrus that is highly selective for faces. The strongest activation in this case is typically an area within the right fusiform gyrus. However, several other areas are routinely found to be more activated for faces than objects, including areas within the left fusiform gyrus, bilateraly in the anterior fusiform gyrus (Gauthier et al., 1999a; Sergent & Signoret, 1992), the left posterior inferior temporal gyrus (Gauthier et al., this issue), and in the medial occipital lobe (Gauthier, personal observation). Recently, Puce, Allison, Bentin, Gore, and McCarthy (1998) have identified an area of the human superior temporal sulcus (STS) that responds to gaze direction and mouth movements.

The multiplicity of areas that show some degree of selectivity for faces in both the human and monkey makes the task of finding homologue regions particularly difficult. (This is not just a problem limited to high-level visual areas—see Kaas, 1995.) Because of the unavailability of cytoarchitectonic and connectivity data in humans, the evidence is mostly restricted to the functional properties of different areas. Given this limited information, we will consider two possible homologies between the human and monkey face processing systems. The first is a region in the STS of both humans and monkeys, which appears to be important for the processing of eye gaze and other facial expressions. The second is an area of the fusiform gyrus in humans and its putative homologue in areas TEa and TEm, which may be important for the identification of individual faces.

FACE CELLS IN THE UPPER BANK OF STS

In general, cells that respond to facial expressions and gaze direction are mostly located in the upper bank and fundus of the STS (Hasselmo et al., 1989; Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1991). Most of these face neurons were found to be 2 to 10 times more sensitive to faces than to simple geometrical stimuli or three-dimensional objects (Perrett, Oram, Hietanen, & Benson 1994; Perrett, Rolls, & Caan, 1979, 1982). They show considerable translation and position invariance, but their response is affected when a three-dimensional head is rotated around the vertical axis (they are somewhat insensitive to rotations in the picture plane). A detailed analysis by Perrett and his colleagues (Perrett et al., 1985, 1994) revealed a total of five types of cells in STS, each maximally responsive to one view of the head. The five types of cells were separately tuned for full face, profile, back of the head, head up, and head down. In addition, two subtypes have been discovered that respond only to left profile or only to right profile, suggesting that these cells are involved in visual analysis rather than representing specific behavioural or emotional responses. The viewpoint selectivity of these neurons is preserved independently of very large changes in lighting. For instance, a cell may respond more to a front view than a profile view regardless of whether the faces are illuminated from a front, top, bottom, or side light source (Hietanen, Perrett, Oram, Benson, & Dittrich, 1992). Masking out or presenting parts of the face in isolation revealed that different cells respond to different features or subsets of features. For most cells in the upper bank of the STS, different faces fail to elicit differentiated activity of the cells, suggesting that this cell population was encoding the object "face" rather than specifying the presence of particular faces. However, a small proportion (10%) of the view-selective face cells in this area appear to show some sensitivity to differences between individual faces (Hietanen et al., 1992).

Lesion experiments in monkeys (Heywood & Cowey, 1992) first revealed that removal of the cor-

tex in the banks and floor of the rostral STS of monkeys results in deficits in the perception of gaze directions and the facial expression, but not in face identification. A later study (Eacott, Heywood, Gross, & Cowey, 1993) found that similar lesions can result in a marked impairment in learning novel visual discriminations (rather than for performing preoperatively learned discriminations as in the 1992 study), but this deficit was not selective for face or eye gaze discriminations.

Perrett and colleagues (1992) have suggested that STS face cells may signal "social attention," or the direction of another individual's attention, information clearly crucial in the social interactions of primates. A possible human homologue for this population of face cells has recently been described by Puce et al. (1998). These authors found that an area in the human STS (posterior portion of the straight segment of the STS) is involved in the perception of gaze direction and mouth movements, but not the perception of comparable nonfacial motion. Puce et al. also note that a number of neuroimaging studies have reported activation in adjacent areas for the perception of different types of biological motion (e.g. lip-reading or body movements).

FACE CELLS IN THE LOWER BANK OF STS

In general, face-selective neurons responsive to the identity of faces are found in a region straddling the lower lip of the STS, in areas TEa/m (Hasselmo, Rolls, & Baylis 1989; Young & Yamane, 1992). These face cells generalise over retinal position but are sensitive to orientation and size to a larger extent than cells in the upper bank of the STS. They show the same type of orientation tuning as Elaborate cells (K. Tanaka, Saito, Fukada, & Moriya, 1991), which respond to moderately complex features such as a vertically striped triangle. To the extent that Elaborate cells may be thought of as shape primitives appropriate to represent nonface objects, the face cells interspersed among them may

be thought of as features appropriate to the representation of different faces.

Hasselmo et al. (1989) studied face cells with a set of nine stimuli consisting of three different monkeys each displaying three different expressions. Neurons were found to respond to either dimension independently of the other. Interestingly, cells responding to expressions clustered in the STS whereas cells responding to identity clustered in area TE. Cells in area TEm showed effects of both dimensions. A quantitative study using correlation analysis between the quantified facial features and the neurons' responses showed that anterior IT face neurons can detect combinations of the distances between facial parts such as eyes, mouth, eyebrows, and hair (Young & Yamane, 1992). These cells show a remarkable redundancy of coding characteristics, as becomes evident from the fact that two dimensions were already found to be enough to explain most of the variance in a population of studied neurons. For example, all the width measurements, such as the width of the eyes or the mouth, the interocular distance, etc., covary with the general width of the face. Moreover, the neurons responsive to faces exhibited graded responses with respect to the face stimuli, with each cell appearing to participate in the representation of many different faces (Young & Yamane, 1992). In comparison, a population of face neurons in the upper bank of STS also exhibited a graded representation of the face stimuli but this population seemed to encode familiarity with the faces (and possibly some other social properties of the stimuli, such as dominance) rather than their physical characteristics. Face-selective neurons are remarkably sensitive to changes in facial configuration, and their response diminishes significantly if facial features are reduced or their spatial relationship is changed. Faces are not the only objects that elicit selective responses in this area. For instance, some cells in inferotemporal cortex also respond to the sight of the entire human body or of body parts (Wachsmuth, Oram, & Perrett, 1994). About 90% of these neurons responded to the human body with responses being selective for certain views, whereas the rest responded equally well to any view of the

stimulus. An intriguing finding, which may lead one to question the simplistic view of "social" face cells in the upper bank of the STS and identity face cells in the lower bank of the STS, is that of cells in area TEa that seem to code for actions. These cells were selectively activated for different instances of certain actions of the hand (e.g. only for manipulate, pick, or tear), and for many of the cells, the responses were independent of the object acted upon (Perrett et al., 1989).

In summary, face cells respond to faces significantly more than to any other visual stimulus (they respond at least twice as much, and often more, to faces compared to the best nonface stimuli). Although they show considerable position and translation invariance, they also exhibit selectivity for rotations in depth or in the picture plane. Most importantly, they appear to encode holistic information, as the entire configuration of a face is often critical for the neuron to discharge action potentials. At this point, population of face cells in TEa/m (lower bank of STS) represents the most likely homologue of the human fusiform face area, since these cell populations are thought to provide distributed representations about face identity (Rolls & Tovée, 1995; Young & Yamane, 1992).

METHODOLOGICAL ISSUES

A few technical aspects of single-cell recording may be worth pointing out to some readers who may primarily be familiar with brain imaging techniques in humans. A limitation of single-cell recording is that researchers are limited to recording from only a small part of the brain at any one moment (in contrast to brain imaging techniques with poorer spatial resolution but a much larger field of view). In addition, there is no way to record systematically from a large and representative sample of neurons of a given brain area: One is more or less dropping a microphone slowly into a pool of firing cells until a single voice can be heard and isolated as an individual cell. Then, an experiment can begin in which the response of the cell is examined under a variety

of conditions (for instance, its response to various visual stimuli). The experiment with this particular cell can proceed until the cell is lost (usually because of cell injury), in which case the experimenter can start looking for another "subject." These technical aspects are important because they limit some of the interpretation of the findings obtained by single-cell recording. That is, to characterise the response of a brain area that would be very homogeneous and would contain cells with identical properties, interrogating just a small number of them would be sufficient. Unfortunately, most brain areas are not homogeneous: In particular, the organisation of IT has been shown to be strongly modular. For instance, the preferred stimuli of different cells within a small cortical column of cells tend to be similar and there is a wide range of optical stimuli for different cortical columns in the same area. Even in areas TEa and TEm, only about 20% of the cells respond to faces. This makes it difficult to record from a large number of face cells. Given that faces are only one of the several categories that an animal may encounter, 20% is a very large representation and this could be due to the particular importance of faces to primates. The approach taken in the experiments described later on is to provide monkeys with extensive training at discriminating members of a particular object category. As the category gains importance for the monkey and as an animal becomes capable of very fine discriminations, this may lead to a more important representation of this category in IT.

Another methodological constraint is that the measured selectivity of any cell depends directly on the set of stimuli that it is confronted with. It is possible faces are over-represented in the sets of stimuli used in many experiments. As an example, Mikami, Nakamura, and Kubota (1994) report having used 411 photographs of human faces, 308 photographs of monkey faces, and 35 nonface objects as stimuli. They found that 45% of stimulus-selective neurons (responding to less than 20% of the stimuli tested) responded to human faces, 29% to a monkey face, 7% to food, 9% to a nonfood object, and 10% to simple geometric shapes. It is difficult to know what to make of these numbers given the biased representation of faces in the stimulus set.

## NEURONS SELECTIVE FOR COMPLEX VIEWS OTHER THAN FACES

Face cells may be greatly represented within IT because faces are one of the few categories of visually similar objects that a monkey needs to discriminate. Consistent with this idea, more face cells in lab-reared monkeys are found to respond to human faces than monkey faces and cells often show better responses to familiar than unfamiliar humans (Mikami et al., 1994). This anecdotal evidence suggests that experience in discriminating visually similar objects of a novel category could lead to more neurons being devoted to this category. Logothetis and Pauls (1995) and Logothetis, Pauls, and Poggio (1995) addressed this question by generating expert monkeys on two different object classes. They used the same wire-like and spheroidal objects (Fig. 1) that had been studied previously in human psychophysical experiments (Buelthoff & Edelman, 1992; Edelman & Buelthoff, 1992).

The animals were trained to recognise novel objects presented from one view and were then tested for their ability to generalise recognition to views generated by rotating the objects mathematically around arbitrary axes. More specifically, successful fixation of a central light spot was followed by the *learning phase*, during which the monkeys were allowed to inspect an object, the *target*, from a given viewpoint arbitrarily called the *zero view* of the target. The learning phase was followed by a short fixation period, after which the *testing phase* started. Each testing phase consisted of up to 10 trials. The beginning of a trial was indicated by a low-pitched tone, immediately followed by the presentation of the test stimulus, a shaded, static view of either the target or a *distractor*. Target views were generated by rotating the object around one of four axes: the vertical, the horizontal, the right oblique, or the left oblique. Distractors were other objects from the same or a different class. Two levers were attached to the front panel of the monkey chair, and reinforcement was contingent upon pressing the right lever each time the target was presented. Pressing the left lever was required upon presentation of a distractor.

After the monkeys mastered the task, they were tested for generalising recognition with a variety of objects, including pictures of real objects (e.g. cars, airplanes, fruits), and wire-like and spheroid objects. In contrast to real objects, the recognition of the novel objects was strictly view-dependent. The monkey could correctly identify the views of the target around the trained view, whereas its performance dropped to chance levels for disparities larger than approximately 40° of rotation in depth. For many wire-like objects the animal's recognition was found to exceed criterion performance for views that resembled "mirror-symmetrical," two-dimensional images of each other, due to accidental lack of self-occlusion. Initially, the animal's generalisation of recognition was also view-dependent for rotations in the picture plane. However, in the latter case recognition performance improved, and in a few sessions it became rotation-invariant.

Recording from the anterior inferotemporal cortex (mostly in the upper bank of the anterior medial temporal sulcus) during this recognition task revealed a number of cells that were highly selective to familiar views of these recently learned objects (Logothetis & Pauls, 1995; Logothetis et al., 1995). These cells exhibit a selectivity for objects and viewpoints that is similar to that found in face cells. The response of many object-selective neurons was invariant for translations within the foveal region (centre 5°) and large changes in size (often by a factor of four in a linear dimension).

To determine the features driving the neural responses, Jon Pauls developed a method in our laboratory of eliminating, scrambling, or occluding the displayed wire segments (Pauls, 1997). By systematically reducing the complexity of the stimulus with this technique, Pauls found that some cells were actually selective to a simple feature such as an angle, rather than to the entire wire configuration. In sharp contrast to such cells, however, other wire-selective neurons exhibited extreme sensitivity to alterations of the stimulus configuration. In other words, reduction of the stimulus was impossible without significantly reducing the unit's response. Almost all view-selective neurons were recorded around the anterior mediotemporal sulcus (Fig. 3).
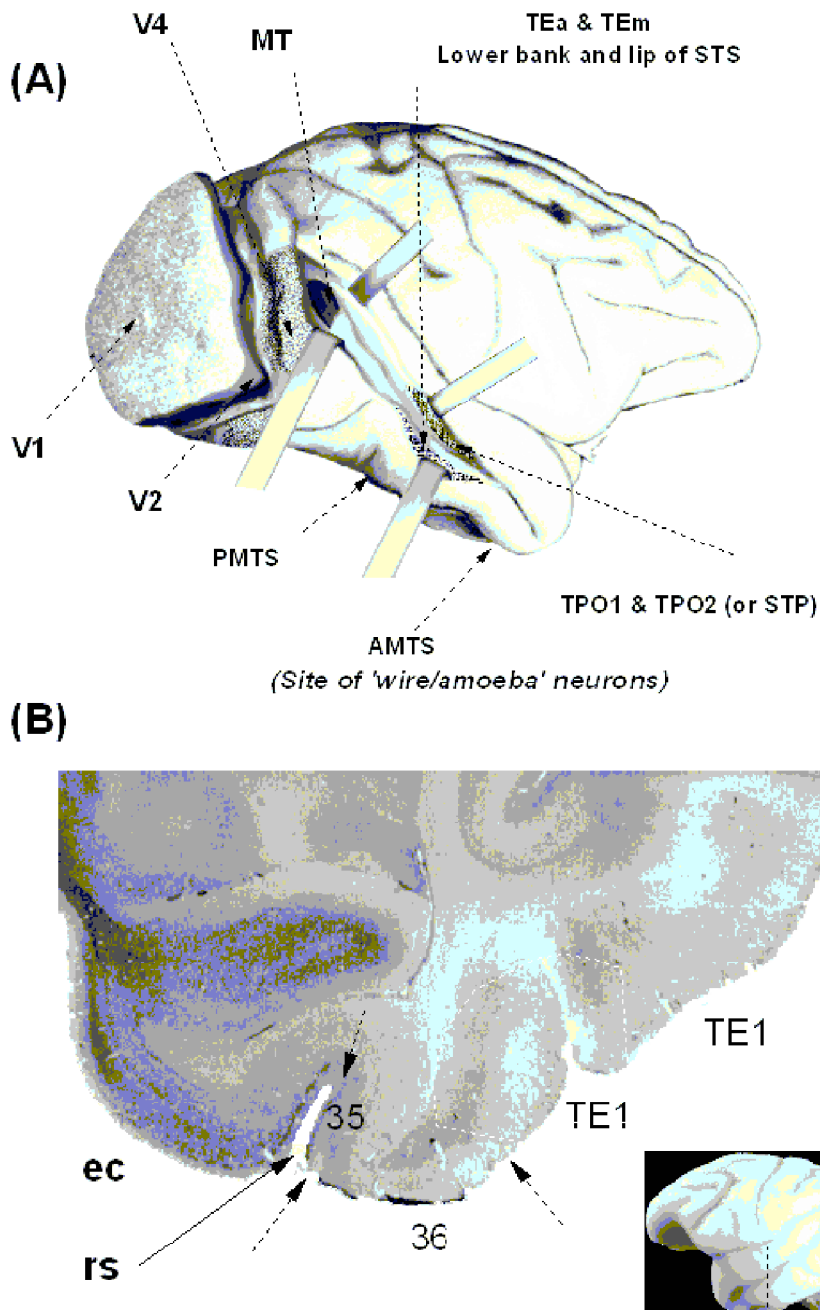
Fig. 1. *Lateral view of a monkey's brain and location of the wire–selective neurons. A. Lateral view with the superior temporal sulcus (STS) opened up to illustrate various visual areas in the temporal pathway. V1, primary (striate) cortex; V2, V4, second and fourth visual areas; MT (or V5) middle temporal visual area; PMTS, posterior mediotemporal sulcus; AMTS, anterior mediotemporal sulcus; TEa/m areas within the inferotemporal cortex; TPO1/2 areas within the STS. B. Histological slice showing the anatomical site in which the wire/ amoeba selective neurons were found: ec, entorhinal cortex, 35/36 areas 35 and 46 respectively (perirhinal cortex); rs, rhinal sulcus. The vertical line depicts the position of the coronal section shown in (B). The arrows depict approximately the borders of the corresponding areas.*
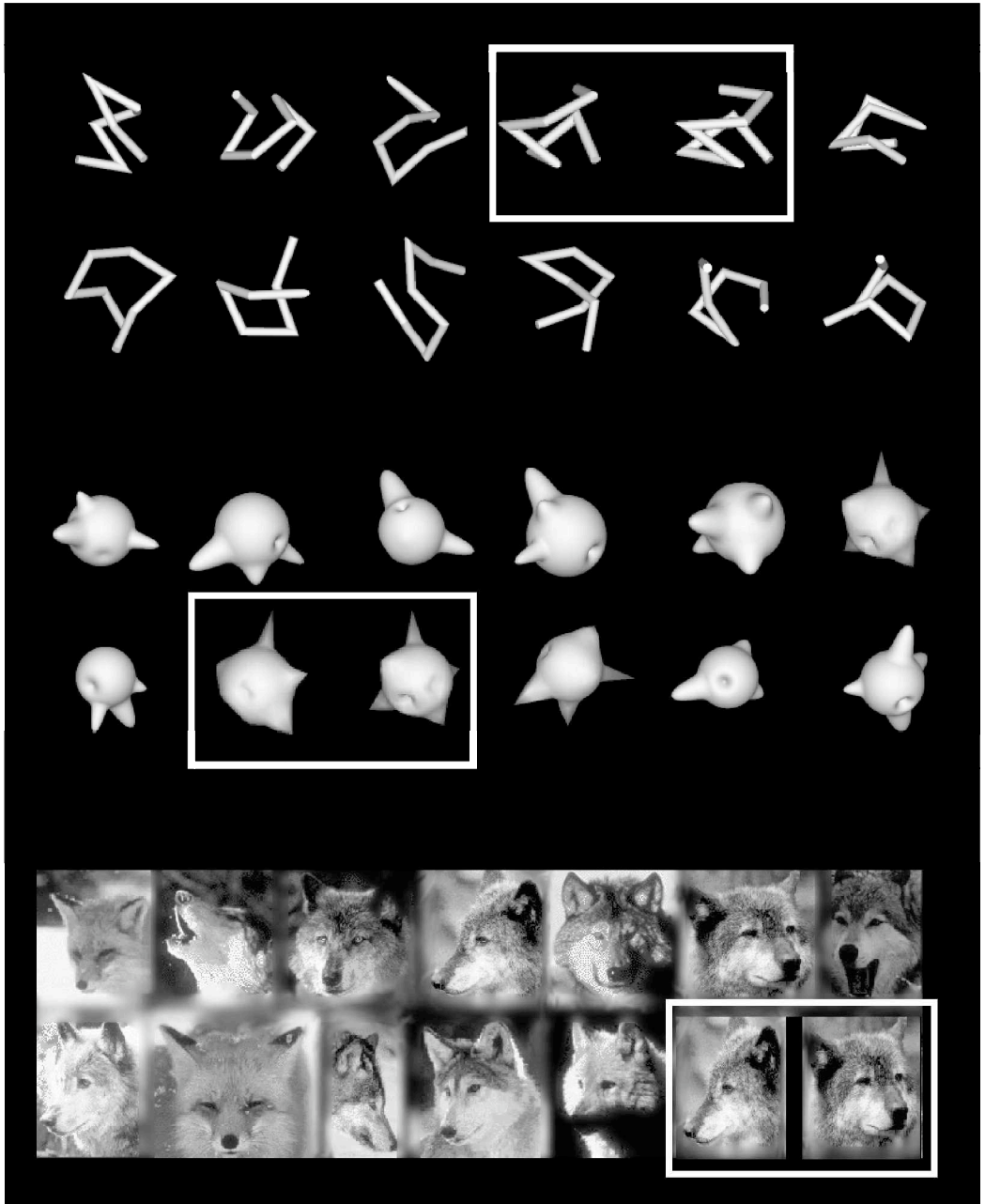
Fig. 2. *The wire- and amoeba-like objects used to study the neural representations that may be employed for recognising objects at the subordinate level. The exemplars of both classes are different barring the two within each white rectangle, which are two views of the same objects 90° apart. Recognising individual exemplars of these classes is not unlike recognising individual exemplars of other homogeneous natural classes. The wolves in the last row are all different barring those within the white rectangle. Again, the latter are two views of the same animal 90° apart. In each case, identification of a member requires excessive practice.*
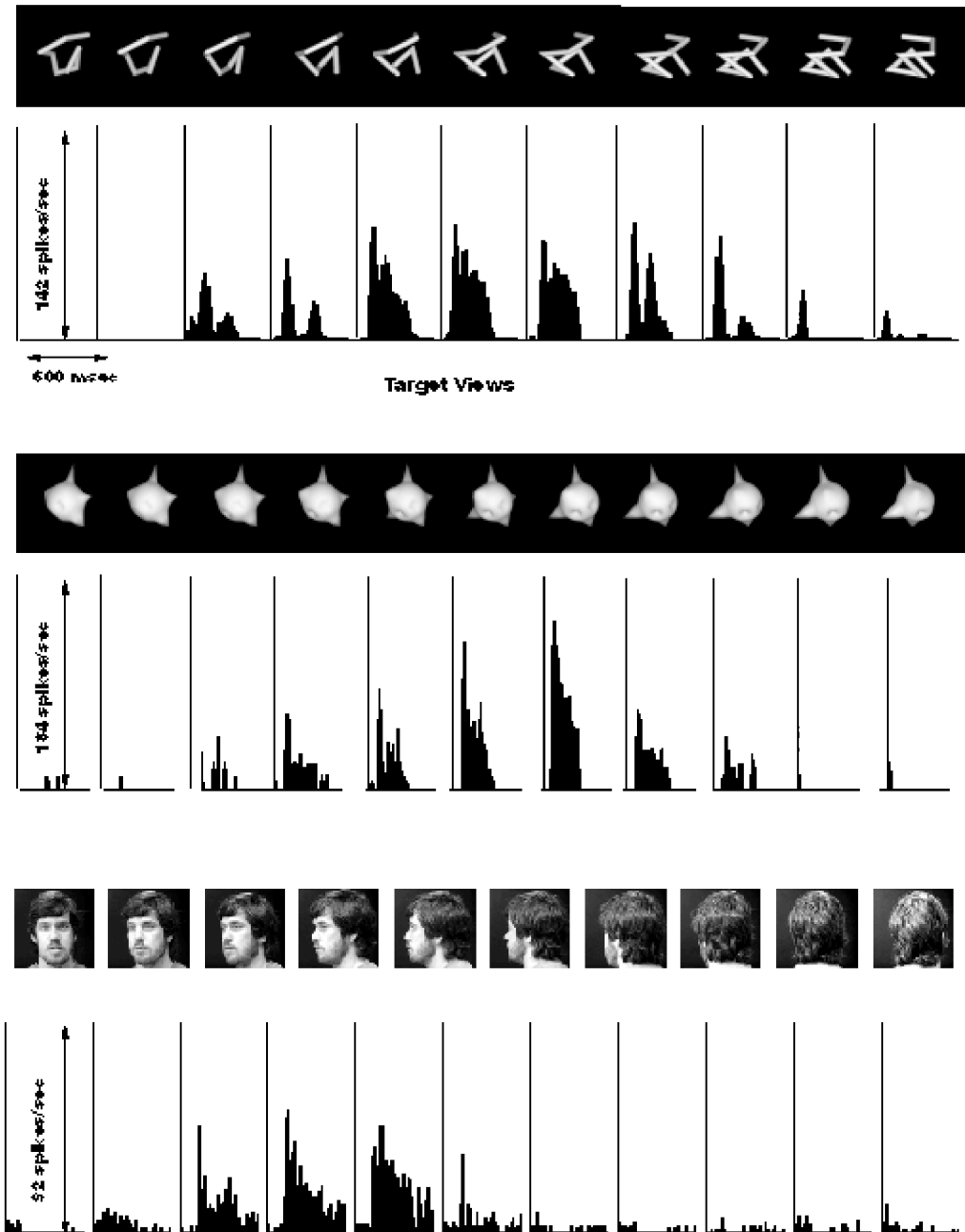
Fig. 3. *Responses of single units in the inferior temporal cortex of the monkey. The upper row shows responses to wire–like objects and the middle row to amoeba–like objects. The neuron responds best to a recently learned object –view and its response diminishes as the object is rotated in depth. For objects that the monkey could recognise from all vantage points more than one unit was found that responded to different views of the same object. Systematic decomposition of the wire objects showed that while some neurons could also be activated by parts of the object (e.g. an angle), others required the entire configuration, strongly diminishing their response even when only a single wire–segment was removed (Pauls, 1997). The bottom row shows responses of a face–selective neuron recorded in the upper bank of the STS. "Wire" and "amoeba" cells display view tuning similar to that of the face cells.*

IS FACE PROCESSING UNIQUE?

The finding of "expert" cells in monkeys trained to discriminate among amoebas and wires suggest that face recognition may find its homologue in the brain under the right circumstances. In Hay and Young's (1982) framework, one way in which faces may be special is that they could be represented in a different manner to nonface objects. In humans, evidence for unique face processing comes from a number of behavioural effects that are obtained with faces but not with nonface control stimuli such as houses and even inverted faces. Most of these behavioural effects measure some aspect of what is called holistic or configural processing. Simply stated, face recognition is often found to be more sensitive than nonface recognition to the disruption of the configuration of features: for instance, moving the eyes slightly apart or inverting the entire face so that relations such as "top of" or "right of" are changed (for reviews, see Farah, 1996; J.W. Tanaka & Gauthier, 1997). Evidence against face processing being unique comes from experiments where the same configural effects are obtained with nonface objects when subjects are experts with these categories (Diamond & Carey, 1986; Gauthier & Tarr, 1997; J.W. Tanaka & Gauthier, 1997). This suggests that configural sensitivity is not restricted to faces and that it is the particular experience with an object category, rather than its superficial properties, which determines the processing of its exemplars. Here, we consider whether IT cells may be thought to represent faces in a different way to other objects.

Face Cells Show a High Degree of Selectivity to the Face Category

Face cells in anterior IT are sensitive to configuration of features (Young & Yamane, 1992) and may be mediating the configural sensitivity that is a hallmark of upright face recognition. In a paper discussing face specificity in humans, Farah et al. (1998) cite the existence of face cells as converging evidence for faces being represented in a different fashion, because "the selectivity and strength of such responses [to nonface objects] are weaker [than to faces]". In a recent review article, Tovée (1998) notes that face cells are resistant to a stimulus simplification protocol (K. Tanaka, 1997) whereas the selectivity of most other IT cells can be reduced to rather simple stimuli. Tovée argues that "The 'specialness' of the face processing system will rest upon the determination of whether the face processing cells in IT have no functional equivalent counterparts for object processing, either in IT or elsewhere."

The single-cell recording experiments described in this paper may provide some evidence for nonface object cells that are the functional equivalent of face cells. A remarkable similarity exists between the properties of the face cells and those of the wire- or amoeba-selective neurons recorded from expert monkeys (Logothetis & Pauls, 1995; Logothetis et al., 1995). The latter type of neurons show selectivity to complex configurations that cannot be reduced without diminishing the cells' response to specific views and to views that appear to be mirror symmetrical. They also exhibit position and scale invariance, and are clustered in a specific brain location. This evidence is consistent with the possibility that the responses of IT cells are built from experience and adapted to the interactions of an animal with objects. In most cases, animals need to recognise most objects at a categorical level (e.g. cage, ball, tree) and faces at the exemplar level. However, if animals need to treat other objects like faces and discriminate visually similar exemplars, a number of cells within IT may begin to represent the features that are best suited to this task.

Face Cells Represent Face Identity in a Sparse Fashion

Several authors (Rolls & Tovée, 1995; Young & Yamane, 1992) have suggested that IT face cells may be representing face identity using sparse coding. On a continuum from "grandmother" representations (where a single cell represents a single object) to highly distributed processing (in which a very large number of cells contribute to the representation, each one carrying an infinitely small amount of useful information), sparse coding constitutes a case where the firing of each neuron

strongly biases the probability of a response to an object. Face cell populations are thought to use sparse rather than distributed coding because each face cell at least carries a lot of information at the level of the stimulus class, responding more to any face than to nonface stimuli. Within the class of faces, however, the cells respond to many of the faces in a more distributed fashion. This type of representation has been suggested to be ideal for the discrimination of faces (Rolls & Tovée, 1995). Note that such conclusions are based on what is called information theoretic analyses, in which face-selective cells are first selected and later shown to provide more information about faces than about nonface stimuli. A comparable analysis for nonface objects would first require the selection of a population of cells that respond best to a certain class of nonface objects than to other stimuli. As discussed previously, this may be impractical for nonface categories of no particular relevance to an animal but may be feasible after an animal has been trained to discriminate among visually similar objects.

Some authors emphasise the similarities between face cells and other IT cells selective for elaborate features. For instance, Perrett and Oram (1993) note that in the anterior temporal cortex, both face cells and Elaborate cells do not generalise across orientation and size (whereas face cells in STP do). In both cases a rotation of 90° in the picture plane reduces the response by more than 50%. However, other authors have contrasted the apparent sparse coding for faces to the more distributed coding by which nonface objects appear to be represented. K. Tanaka (1997) has suggested that nonface objects are represented by distributed coding over a large number of IT columns, each containing cells selective for moderately complex features. In this framework, each shape primitive carries very little information about the identity of the object and the representation of nonface objects may be argued to be qualitatively different from that of faces, in that it would be considerably more distributed.

Recently, however, Kobatake, Wang, and Tanaka (1998) have trained monkeys to recognise 28 moderately complex stimuli (mostly combinations of 2 simple geometric shapes, these stimuli were less homogeneous than wires or amoebas) and found a greater proportion of cells responsive to the trained stimuli in trained than untrained monkeys. Furthermore, many of these cells responded to multiple members of the training stimuli, not unlike face cells. The discriminations learned by the monkeys may be supported by sparse representations and the number of cells that respond to a certain object may be partly determined by an animal's experience with this category (see also Booth & Rolls, 1998). However, experience with a visually homogeneous class of objects (e.g. the wires and amoebas) may be necessary to build up a population of cells that will generalise to novel exemplars of the category. When humans are trained with several objects of an homogeneous category, their expertise generalises to novel exemplars (for instance, configural sensitivity is found for untrained objects—Gauthier & Tarr, 1997). Given the similarity of behavioural performance in object recognition tasks between man and monkey (Logothetis & Pauls, 1995), we can hypothesise that expertise in monkeys would also generalise to novel exemplars of a trained class. However, such generalisation could be expected in monkeys trained with ameobas and wires, but not necessarily for animals trained with less homogeneous stimulus sets.

IS FACE PROCESSING SPECIFIC?

Even if we found that faces and objects are represented by common mechanisms in IT, faces could still be special in that they could be processed in a distinct and separate neural system. It may be that *specificity* (Hay & Young, 1982) in the location of cells for any object category is not a sufficient criterion to designate this category "special" (Tovée, 1998), presumably because specificity would not be unique to a single category (i.e. if face cells are separated from wire cells, then wire cells are also separated from face cells). However, regardless of the debate on faces, to consider the spatial organisation of object-selective cells is essential to the understanding of the temporal cortex organisation.

The area where wire and amoeba cells were found, the AMTS, is anterior to area TE and more

ventral than areas where face cells are typically found in other studies. What this means is somewhat difficult to interpret, given the methodological constraints of single-cell recording. As in any single-cell study where there is no prior knowledge of precisely where selective responses are expected, Logothetis and colleagues (Logothetis & Pauls, 1995; Logothetis et al., 1995) recorded systematically from posterior to anterior areas of the temporal lobe, moving to a new area after a week or so of fruitless explorations. Once a first wire- or amoeba-selective cell was found in AMTS, the researchers kept on recording in this area without going back to more posterior regions. In addition, the AMTS was not systematically tested with faces in this experiment. In other words, the current evidence suggests that populations of expert object cells are found in a different area than populations of face cells with comparable properties, but this evidence is not as strong as it would be if it came from a neuroimaging experiment in which all areas of the visual system had been equally sampled at all time-points.

Evidence that face processing may be segregated from object processing in the human brain mainly comes from two different sources. The first is evidence from patients with selective deficits in face processing (De Renzi, 1986; Farah et al., 1995a). The selectivity of face agnosia is controversial, as many prosopagnosic patients also report difficulties with other visually similar categories (Bornstein, Sroka, & Munitz, 1969; Damasio et al., 1982; Shuttleworth, Syring, & Norman, 1982). Even in the case of patients who believe that their deficit applies only to faces, recent work has revealed a more general impairment for subtle, subordinate-level discriminations (Gauthier et al., 1999b). A second source of evidence comes from neuro-imaging studies in which activation in the middle fusiform gyrus is found when subjects are viewing faces as opposed to nonface objects (Kanwisher et al., 1997; McCarthy et al., 1997; Sergent & Signoret, 1992). To address this evidence and inspired by the fact that prosopagnosic patients often have difficulties discriminating objects within the same category, Gauthier et al. (1998) compared brain activation when normal subjects verified the subordinate identity of a picture (e.g. *pelican*) vs. the basic level (e.g. *bird*). They found activation in ventral temporal areas described as face-sensitive in prior studies. In this issue, a new study (Gauthier et al., this issue) verified that subordinate-level processing of nonface objects activates the small area that can be defined as face-specific in each subject. Thus, the presentation of faces is not necessary to engage what is often called the "face area." This region can be differentially engaged when the same nonface object is recognised at the subordinate vs. the basic level. However, faces appear to activate only a portion of ventral cortex dedicated to subordinate-level processing. These studies, which suggest that subordinate level processing accounts for *some* of the activation in the face area, are not necessarily incompatible with other work suggesting that *not all* of the activation in the face area can be accounted for by subordinate-level classification (Kanwisher et al., 1997). What may be happening is that the former studies focus on the fact that there is difference between basic level and subordinate level recognition of nonface objects in the face area, whereas the latter studies account for a different part of the data, pointing out that there is still more evidence for subordinate-level recognition of faces than subordinate-level recognition of nonface objects. A recent fMRI study (Gauthier et al., 1999a) has revealed that expertise with subordinate-level discrimination of novel objects (similar training experience as the monkeys in Logothetis & Pauls, 1995; Logothetis et al., 1995) leads to increased activation localised in the "face area." This suggests that the interaction of two factors, level of categorisation and expertise, may interact to produce the specialisation for faces found in the middle fusiform face area. In the next section, we consider how what we know of the monkey visual system can help resolve the role of these two factors.

Level of Categorisation and Expertise

Given the importance of level of categorisation demonstrated in behavioural (J.W. Tanaka & Taylor, 1993) and fMRI studies in humans (Gauthier et al., 1998, this issue), one may ask whether there is any evidence that this factor is important in

determining the responses of IT cells. Unfortunately, no single-cell recording study has compared the responses of cells to the same stimuli when animals are requested to recognise it at different levels of abstraction. However, Logothetis and Pauls (1995) have trained monkeys to recognise objects either at the basic level (among distractors differing largely in shape, such as a wire vs. an amoeba) or at the subordinate level (for instance, discriminating between two wires). They found that the animals' behavioural performance was viewpoint-dependent in the case of subordinate-level judgements and viewpoint-independent in the case of basic-level judgements. This suggests that level of categorisation may at least have a similar importance for monkey and human visual recognition.

Two recent studies provided monkeys with experience with certain objects and later found cells to be responsive to many of these trained objects (Booth & Rolls, 1998; Kobatake et al., 1998). However, these studies differ in an important way from the wire-frame and amoeba study by Logothetis and colleagues: The different objects did not belong to what would be considered the same "basic-level" category (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). This is because they do not share common parts and could be discriminated by the presence of a single feature (e.g. the way that the presence of eyes is diagnostic to detect a face) or simple relationships between parts (e.g. as for the presence of a nose underneath two eyes). In comparison, objects from homogeneous categories share common parts as well as the first-order configuration of these parts (Diamond & Carey, 1986; Rhodes & McLean, 1990). They can only be distinguished using subtle differences in the shape of their parts or subtle differences in the configuration of their parts (e.g. distances between different face features). It is expertise discriminating between objects of such homogeneous categories that is thought to mediate behavioural configural effects and the increased recruitment of the fusiform face area (Gauthier & Tarr, 1997; Gauthier et al., 1999a). Again, there is yet no direct comparison using physiological measurements of the difference between basic and subordinate level processing of objects, but the expertise of monkeys discriminating between wires and amoebas may be most relevant to the debate on face recognition in humans.

In humans, recent fMRI results suggest that expertise with novel objects (Greebles) can recruit the middle fusiform face area (Gauthier et al., 1999a). However, at least one area, in the lateral occipital gyrus, showed a strong expertise effect, with more activation for Greeble experts than novices, and even more for Greebles than for faces. This lateral occipital gyrus area did not behave like the fusiform face area in all conditions: In particular, this region responded more to inverted than to upright faces, whereas the face area responded more to upright than to inverted faces. Thus, there may be a complex system of areas within the temporal lobe that is modified by experience with objects. This is consistent with the existence of face cells in many areas of both the human and the monkey brain. Similarly, AMTS may not be the only area of expert monkeys where wire and amoeba cells can be found. At this point, it is likely that further advances in comparing the man and monkey systems will require the addition of novel techniques such as functional MRI in monkeys (Logothetis, Guggenberger, Peled, & Pauls, 1999) to those already available in both species.

CONCLUSIONS

Both humans and monkeys are extremely good at recognising faces, a fact that is hardly surprising in view of the vital importance that face recognition has for the primate. An important neural system exists in both species for the processing of facial information. In the human behavioural literature, starting with Diamond and Carey's (1986) landmark study of dog expertise, a consensus has grown that nonface categories of objects can be processed in the same way as faces given similar task constraints and subject expertise. However, in human neuropsychological and neuroimaging studies, there is still an ongoing debate regarding the possibility that faces may be special.

Interestingly, the single-cell recording literature also converges to suggest that faces are not repre-

sented by IT cells in a unique fashion. Several authors, including C.G. Gross (1992), the pioneer in the domain of face cells, have suggested that face cells may appear more specialised than other IT cells only because face recognition happens to be an extremely demanding subordinate recognition task, and for nonhuman primates it may be the only identification task performed in life. Clearly, such an hypothesis leads to the prediction that a similar specialisation may also arise when the identification of members of other classes becomes the critical task at hand. This was tested in recent single-cell recording experiments. A remarkable similarity was found between the properties of the face cells and those of the wire- or amoeba-selective neurons recorded from expert monkeys (Logothetis & Pauls, 1995; Logothetis et al., 1995). The latter type of neurons show selectivity to complex configurations that cannot be reduced without diminishing the cells' response to specific views and to views that appear to be mirror-symmetrical. They exhibit position and scale invariance, and are clustered in a specific brain location. Since recordings have only been made in the inferotemporal cortex and mostly in AMTS, it is not currently known whether selectivity to these objects might not also be found in other brain structures.

Such results are consistent with behavioural and fMRI studies in humans showing that novel objects are processed in a more configural manner with expertise and can increasingly recruit parts of the ventral temporal lobe. However, whereas fMRI results in humans suggests that the very same areas are recruited for faces and nonface objects, single-cell studies in monkeys point to specialisation of different areas. These techniques are very different and it is important to note that fMRI could provide more convincing evidence than single-cell data for a *dissociation* between the location of face and object expert processing. On the other hand, the better spatial resolution of single-cell recording could provide stronger support for an *association* in location (e.g. if the very same cells were found to mediate expert representations of different categories). Paradoxically, the current data in fMRI suggests an association whereas single cell recording suggests a dissociation, albeit only in the location of

face and wire/amoeba cells within the anterior temporal lobe. Therefore, for both sources of evidence the interpretation should be cautious. In any case, faces are not unique with regard to the type of neural activity that can be recorded in a monkey's brain when the animal is coping with other classes of objects in the same manner with which it deals with faces.

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