

Representation of visual stimuli in inferior temporal cortex

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SUMMARY

In primates, inferior temporal (IT) cortex is crucial for the processing and storage of visual information about form and colour. This article reviews the properties of IT neurons and considers how these properties may underlie the perceptual and mnemonic functions of IT cortex. The available evidence suggests that the processing of the facial image by IT cortex is similar to its processing of other visual patterns. Faces and other complex visual stimuli appear to be represented by the pattern of responses over a population of IT neurons rather than by the responses of specific 'feature detectors' or 'grandmother' cells. IT neurons with adult-like stimulus properties are present in monkeys as young as six weeks old.

1. INTRODUCTION

At a meeting of the Royal Society just over 100 years ago, Brown & Schafer (1888) reported that after temporal lobe damage monkeys no longer seemed to understand the meaning of what they saw, although their vision itself appeared normal. These observations were lost in the bitter battle between Ferrier (1888) and Schafer (1888) on the location of the cortical areas for audition and vision. Fifty years later, similar observations on temporal lobectomies were made by Kluver & Bucy (1938). Kluver was led to the temporal lobe by his interest in mescaline (Kluver 1928). On the basis of the mescaline-like hallucinations that often precede temporal lobe seizures, he had speculated that the drug might act on the temporal lobe. Kluver & Bucy termed the visual recognition symptoms that followed the temporal lobectomies, 'psychic blindness'. Subsequent work by Chow and by Pribram and his students, particularly Mishkin and Weiskrantz, made it clear that these visual recognition deficits only follow lesions that include the cerebral cortex on the inferior convexity of the temporal lobe, namely inferior temporal (IT) cortex or cytoarchitectonic Area TE (see references in Gross (1973)).

Inferior temporal lesions severely impair the ability of monkeys to recognize, learn about and remember visual stimuli. They do so in the absence of changes in basic visuosensory functions, such as visual acuity and other visual thresholds, or any deficits in modalities other than vision (Gross 1973; Mishkin 1966, and references cited therein). In 19th century terms, IT lesions produce a visual agnosia (Freud 1891) which has both 'apperceptive' and 'associative' elements (Lissauer 1890). In more modern terms, IT lesions produce a deficit in processing and storing information about form and colour. In humans, a similar

syndrome is also associated with temporal cortex pathology (Milner 1968). The human syndrome often includes deficits in face processing and sometimes such a deficit is the most striking symptom (Damasio 1989).

We begin by reviewing the basic response properties of IT neurons. We then consider whether there is any special relationship between processing of the facial image and IT cortex, and confront the rumour that IT cortex is full of 'grandmother cells'. Next, we consider the ontogeny of IT neuron properties. Finally, we list some unsolved problems about how faces and other visual stimuli are represented and recognized by IT neurons.

2. PROPERTIES OF INFERIOR TEMPORAL (IT) CORTEX NEURONS

1. IT cells respond only to visual stimuli. This dovetails with the exclusively visual effects of IT lesions (Gross *et al.* 1967, 1972).

2. Virtually every receptive field includes the fovea and responses to stimuli at the fovea are more vigorous than elsewhere in the receptive field (Desimone & Gross 1979). These properties mirror the crucial role of the centre of the gaze in form perception. Unlike striate cortex and the various prestriate visual areas, IT has no visuotopic organization.

3. Receptive field size is relatively large (median about 25 deg × 25 deg) as compared with that in 'earlier' visual areas such as striate cortex (V1), V2 and V4 (Desimone & Gross 1979; Gattass *et al.* 1988). Stimulus selectivity remains similar throughout the receptive field, thus providing a basis for perceptual equivalence across retinal translation (Gross & Mishkin 1977). See figure 1*c*.

4. Most receptive fields extend across the vertical

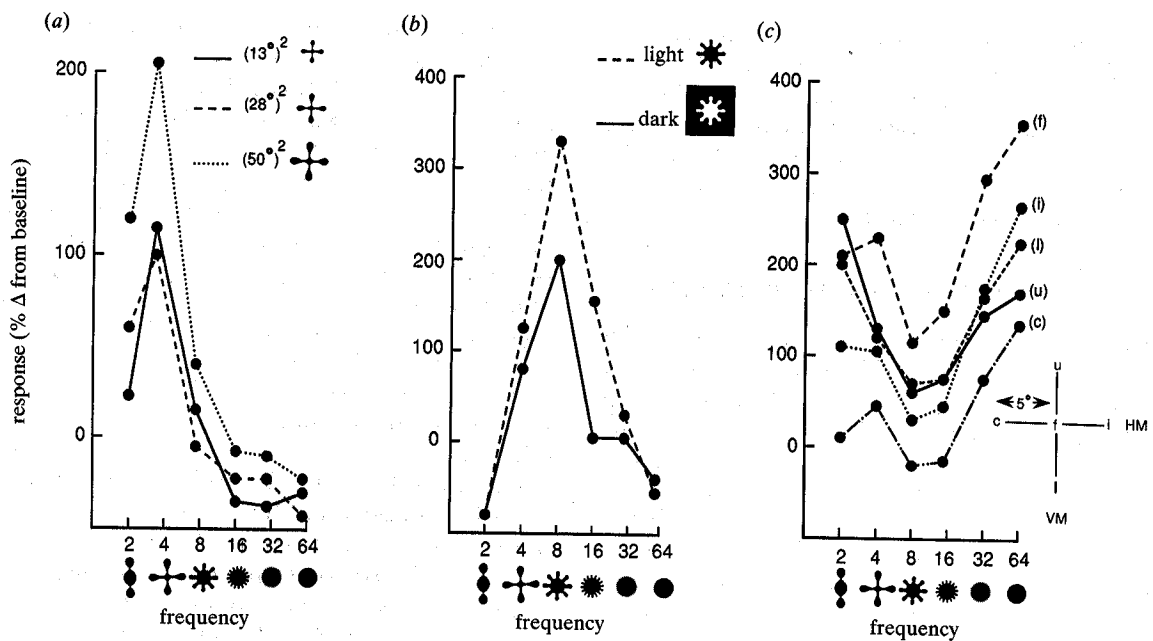


Figure 1. Responses of three IT neurons to a set of shapes. The shape selectivity remains similar over changes in stimulus size (a), contrast (b), and retinal location (c). Responses are plotted as percent change of each neuron's mean spontaneous rate. Each point is a mean of ten responses. Key to symbols: f, fovea; c, contralateral field; i, ipsilateral; u, upper; l, lower. (After Gross *et al.* 1985.)

meridian well into both visual half-fields. Thus, the two halves of visual space are represented in single cells for the first time in visual cortex (Gross *et al.* 1972).

5. Many IT cells are selective for some aspect of shape, texture or colour. A few are selective for more than one of these. Rather than act as narrow filters for a particular stimulus, IT cells tend to respond at different rates to a variety of different stimuli. A small proportion are selective for faces or hands (Gross *et al.* 1972; Desimone *et al.* 1984; Perrett *et al.* 1982; Tanaka *et al.* 1991).

6. Selectivity of many IT neurons for shape is maintained over changes in stimulus size, contrast, and wavelength. That is, they show shape constancy, both for arbitrary geometrical patterns, as shown in figure 1, and for natural ones such as faces (Schwartz *et al.* 1983; Rolls & Baylis 1986).

7. The above 'sensory' properties are found both in awake behaving animals and animals anesthetized with nitrous oxide, but not in animals under barbiturate anesthesia (Gross *et al.* 1972, 1979; Richmond *et al.* 1983).

8. In behaving animals, IT responses can be modulated by recent experience in delayed-matching-from-sample and habituation paradigms (see, for example, Gross *et al.* (1979); Miller *et al.* (1991); Mikami & Nakamura (1988); Rolls *et al.* (1989)). They may also show longer term effects of experience (Miyashita 1988).

9. The response of an IT neuron can be gated by the site of the animal's attention within the cell's receptive field (Moran & Desimone 1985) and by the task relevance of the stimulus (see, for example, Gross *et al.* (1979); Sato 1988).

10. IT cortex is the final stage of the occipital-temporal pathway specialized for the analysis of form

and colour. IT receives visual information from striate cortex over a pathway that includes V2 and V4 as shown in figure 2 (Desimone *et al.* 1980; Ungerleider 1985). The ipsilateral portion of IT receptive fields depends on information from the opposite hemisphere by way of the splenium and the anterior commissure (Rocha-Miranda *et al.* 1975; Gross *et al.* 1977). In anaesthetized animals, the cortico-cortical input is necessary and sufficient for the visual properties of IT cells. However, in the awake animal, input from the tecto-pulvinar system may be important for modulation of attention and receptive field size (Gross *et al.* 1974; Peterson *et al.* 1987; Moran & Desimone 1985).

11. IT cortex may be subdivided on the basis of cytoarchitectonics, connections and receptive field size (Seltzer & Pandya 1978; Desimone & Gross 1979).

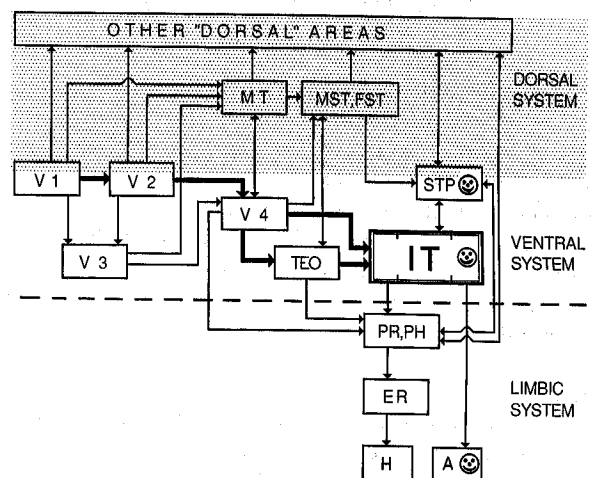


Figure 2. Main afferent routes to IT cortex and some IT-limbic connections.

12. Relatively nearby neurons are more likely to have similar stimulus properties (Gross *et al.* 1972) and to show functional interactions (Gochin *et al.* 1991).

13. As estimated by cross-correlation analysis, the number of synaptic inputs required to drive an IT neuron is typically greater than the number required to activate a striate neuron (Gochin *et al.* 1991).

3. FACE-SELECTIVE CELLS IN IT CORTEX

In 1969 we reported a cell selective for the shape of a monkey hand (Gross *et al.* 1969). When we altered this stimulus in various ways such as adding fingers, rearranging it or changing its size, the magnitude of the neuron's response was unrelated to any physical parameter of the stimulus. Rather, it correlated with the similarity (to us) of the stimulus to a monkey hand. Soon after, we began to find some IT cells that were selective for photographs of faces (Gross *et al.* 1972). Perhaps because of the initial sceptical reaction to the original hand cell report, we waited another nine years to publish any detailed accounts of face selective cells (Bruce *et al.* 1981). By this time, face-selective cells were being actively studied by Rolls and Perrett and their collaborators (e.g. Perrett *et al.* 1982; Rolls, this symposium; Perrett *et al.*, this symposium, and references cited therein). More recently, face-selective cells have been investigated in several Japanese laboratories (see, for example, Yamane *et al.* (1988); Tanaka *et al.* (1991); Mikami & Nakamura (1988)).

IT cells may be classified as 'face-selective' if (i) they respond significantly more to faces than to a variety of other stimuli and (ii) their selectivity for faces remains invariant across changes in size, colour, and contrast. By now, a great variety of face-selective cells have been described. Some respond only or best to a particular face orientation ('viewer-centred') whereas others respond similarly to all orientations ('object-centred'). Some only respond to a complete face, some will show a decline in response when face components (such as mouth or eyes) are eliminated and some will respond to face components in isolation. These and other characteristics of face-selective cells are described in detail by Desimone *et al.* (1984), Rolls (this symposium), Perrett *et al.* (this symposium) and Desimone (1991).

(a) Distribution of face-selective cells

In addition to IT cortex, face-selective cells have been found in several areas that have monosynaptic connections with IT cortex, namely the superior temporal polysensory area (STP) (Bruce *et al.* 1981), the basal accessory nucleus of the amygdala (Rolls 1984), the ventral putamen (Rolls & William 1987) and the arcuate gyrus of the frontal lobe (Pigarev *et al.* 1979). Hand selective cells were also found in the first two of these areas.

Face-selective cells are most numerous in two adjacent areas, the portion of IT cortex on the ventral bank of the superior temporal sulcus (STS) and the portion of the superior temporal polysensory area on the dorsal bank of this sulcus (Baylis *et al.* 1987). In spite

of including similar face-selective cells, these two areas are otherwise quite different from each other. Relative to IT cells, most STP cells (but not the face-selective ones) have even larger receptive fields, do not respond more strongly at the fovea, and are particularly sensitive to complex movement, sometimes including biological movement; about half these cells are responsive to auditory or somesthetic as well as visual stimuli (Bruce *et al.* 1981; Perrett *et al.* 1989). Because there is some evidence that STP plays a role in eye movements and orientation (Colby & Miller 1986; Skelly *et al.* 1989), it is possible that the face-selective cells and the biological movement cells in STP are involved in mechanisms of orientation toward and away from other monkeys.

Lesions of the amygdala result in dramatic changes in social behaviour and the face cells in the amygdala presumably play important roles in such behaviour. The face-selective cells in the frontal lobe are in a ventrolateral area that contains other visual cells (Pigarev *et al.* 1979). This area appears to be an extension into the frontal lobe of the ventral or occipito-temporal system specialized for visual pattern recognition. Ventrolateral frontal cortex is reciprocally connected to IT cortex (Pandya & Kupers 1969) and its removal impairs visual discrimination learning (see Bachevalier & Mishkin 1986). The adjacent frontal area, near the principal sulcus, is involved in 'working' spatial memory, probably in interactions with parietal cortex (Goldman-Rakic 1987). Perhaps the ventrolateral area is involved in working visual memory, in interactions with IT cortex.

(b) Grandmothers, gnostic cells and Thomas Young

Grandmother cells have been both ridiculed as the *reductio ad absurdum* of hierarchical processing and 'proved' by the discovery of hand- and face-selective cells in IT cortex. As first proposed (to make an epistemological point) by Jerry Lettvin, a grandmother cell (actually a 'mother cell' was the example he discussed in detail) represented the concept of a specific grandmother. Such cells were to respond only to the grandmother 'however displayed, whether animate or stuffed, seen from behind, upside down or on a diagonal, or offered by caricature, photograph or abstraction' (Lettvin 1969). By the time the term got into the textbooks and became common usage among neurophysiologists it had become a short hand for the theory that complex images were each represented by the firing of specific dedicated neurons.

A few years earlier a similar view had been worked out in detail by Konorski (1967) in his *Integrative activity of the brain*. Konorski hypothesized a set of 'gnostic units' at the top of each sensory hierarchy (Gross 1968). Gnostic units were neurons that 'represent unitary perceptions'. *Inter alia*, Konorski suggested that in monkeys, visual gnostic neurons were located in inferior temporal cortex, and in humans, prosopagnosia was due to the elimination of face gnostic units. As likely examples of gnostic cells, Konorski gave faces, facial expressions and hands.

The idea of grandmother or gnostic cells is hardly

new. Sherrington (1955) referred to a 'pontifical cell' as the 'climax of the whole system of integration'. Grandmother, gnostic and pontifical cells are all examples of labelled line cells at the top of a hierarchy; labelled lines, in turn, are the modern term for Helmholtz's (1856) Doctrine of Specific Fibre Energies which was an extension to single cells of Muller's (1838) Doctrine of Specific Nerve Energies.

Are there grandmother-gnostic cells in IT cortex? Are there single cells in IT cortex whose firing represents a visual percept? First, we take up the general issue and argue that visual stimuli are represented in IT cortex by the pattern of activity across ensembles of cells and not by the firing of single cells. Second, we take up the specific case of face-selective cells and argue that they are not an exception: they are members of ensembles for coding faces rather than detectors for a particular face.

With the exception of face- and hand-selective cells, there is no evidence for IT cells that are selective for visual objects such as fruit, tree branches, monkey genitalia, features in the monkey's laboratory or natural environment or any other object. IT neurons may well discharge to these and other stimuli but they have not been shown to be particularly selective for them. Of course, it is possible that no one has presented the appropriate stimulus while recording from the appropriate cell. Perhaps as distinguishing among apples, for example, is so much less important for monkeys than distinguishing among faces, apple-detecting cells may be so rare as to make their discovery highly improbable, but unless evidence for them appears, it seems more parsimonious to assume that they do not exist.

The view that IT cells are members of ensembles for population coding is supported by several of their properties (Gross *et al.* 1972; Desimone *et al.* 1984). First, most IT cells are selective for some respect of shape, texture or colour, although it may be difficult to specify the relevant parameter. Second, most IT cells give at least a small response to a number of apparently dissimilar stimuli. Third, some IT cells are selective for shape independent of colour, some for colour independent of shape, and finally some are selective for both shape and colour. Finally, there are severe difficulties with the grandmother-gnostic idea for coding percepts. For example, there are probably more percepts distinguishable by an individual than available cells. Another problem is that the labelled-line idea does not easily cope with coding of the relatedness among stimuli.

The idea of ensemble coding, like the idea of labelled lines, is not a new one. Its first explicit formulation was for colour coding by Thomas Young (1802). As he put in this journal nearly 200 years ago: 'Now, as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance to the three principal colours . . . and that each of the particles is capable of being put into motion less or more forcibly by undulations differing

less or more from a perfect unison . . .'. Although this idea of ensemble coding for colour was subsequently publicized by Helmholtz (1856) and became generally accepted for colour it seems as if it has to be rediscovered for each sensory system, for example, by Weddell (1955) for somesthesia and by Pfaffman for taste (1959).

Are face cells an exception to the view that IT cortex represents the visual world through the pattern of firing across a neuronal ensemble? Are they truly gnostic-grandmother cells? After all, faces are uniquely crucial in primate social behaviour, they are perceived extra-ordinarily early in life, they have special perceptual properties, our memory for them is especially prodigious, and the loss in their perception after cortical damage is probably the most specific and socially disabling perceptual deficit after any brain damage (Young & Ellis 1989). Because of the importance of faces, perhaps evolution has provided special purpose detectors, gnostic-grandmother cells, only for them (and a few other very special stimuli such as hands). Yet, there is no convincing evidence for specific face detectors, that is, for an IT cell narrowly selective for a specific face across transformations of size, orientation, and colour. Even the most selective face cells discharge to a variety of individual faces and usually also discharge, although to a lesser degree, to other stimuli as well. Thus, faces are presumably coded in exactly the same fashion as everything else, namely, by the pattern of firing of ensembles of cells with varying selectivity rather than of individual cells acting as complex feature detectors. On this view, the face-selective cells are all members of ensembles specializing in representing faces.

There are at least two possible reasons why the members of face coding ensembles may appear more specialized than the members of other stimulus encoding ensembles. First, it is more crucial for a monkey to differentiate among faces than among any other categories of stimuli. Second, faces are more similar to each other in their overall organization and fine detail than any other stimuli that a monkey must discriminate among. If there had been strong selective pressure for a monkey to distinguish all the individual leaves of a particular oak tree it would probably have an ensemble for doing so that was made up of cells, each of which were selective for leaves of that species of oak.

(c) *Face-selective cells and prosopagnosia*

Are face-selective cells involved in face recognition? There is actually no evidence that face-selective cells play a role in perceiving and remembering faces, whether as individual detectors or members of an ensemble. That is, both the 'grandmother' and 'ensemble' codes for faces are, at best, 'candidate' codes rather than biological ones (Perkel & Bullock 1968). However, because face-selective cells are probably the most specific and complex visual neuron known and prosopagnosia is probably the most specific and complex perceptual impairment in humans, it is certainly tempting to suggest that it is loss of the

former that results in the latter. Three problems suggest at least a temporary delay in succumbing to this temptation. The first is that prosopagnosia may not be specific to faces. Prosopagnosia is usually accompanied by a difficulty in recognizing closely similar members of a class, such as birds or motor cars (Damasio 1989; but see DeRenzi (1989)). Perhaps, cells adjacent to face-selective ones are specialized for coding of similar stimuli in a particular category, such as birds. The second problem is that, as discussed above, the highest concentration of face-selective neurons is in the superior temporal sulcus and yet the most common lesion associated with prosopagnosia in humans is a (bilateral) ventromedial occipito-temporal one (Damasio 1989). It is possible, however, that the output of face-selective cells courses ventrally on its way to an entorhinal or other limbic cortex destination and would be interrupted by ventral occipitotemporal damage (see figure 2), but there is no evidence for this possibility. Probably the most serious problem about the function of face-selective cells is that in monkeys, lesions of the 'face cell area' in STS do not seem to produce a face recognition deficit, although, as discussed by Heywood & Cowey (this symposium), there are difficulties in making the human and monkey tests equivalent.

One intriguing possible link between monkeys and humans is that some cells in the superior temporal sulcus are selective for direction of gaze (Perrett *et al.*, this symposium) and a deficit in discriminating direction of gaze has been found both in monkeys with STS lesions and human patients (Campbell *et al.* 1990; Perrett *et al.* 1988; Heywood & Cowey, this symposium). Because the monkeys and at least some of these human patients were not otherwise severely impaired in face recognition, different aspects of face processing apparently can be neurally dissociated (Perrett *et al.*, this symposium; Heywood & Cowey, this symposium).

Clearly, more data are required before prosopagno-

sia can be attributed to loss of face-selective cells. Specifically, we need a humanoid prosopagnosia deficit after a removal or disconnection of face-selective cells in the monkey and, if possible, a perceptual effect specific to face recognition from electrically stimulating a cluster of face cells.

4. KANT VERSUS LOCKE

Are monkeys born with cells selective for faces and other complex stimuli as Kant and the Gestalt psychologists would have predicted, or are such cells the result of experience with the visual world as Locke and the behaviourists taught? To begin to answer this question we have been recording from IT cortex in young monkeys (Rodman *et al.* 1991).

We trained infant monkeys to fixate visual stimuli and recorded the responses of IT neurons as they did so. IT neurons in animals as young as five-and-a-half weeks had selective responses to faces, to geometrical patterns, and to other complex stimuli indistinguishable from those found in adults (see figure 3). Under these conditions, we found no sign of any developmental trend toward increased or different responsiveness or selectivity between infancy and adolescence.

To plot accurately receptive field properties in infants we also recorded from them while immobilized and under nitrous oxide anesthesia. Under these conditions, when the IT cells were visually responsive, we found their receptive fields and stimulus selectivity to be similar to those in adult animals. However, in these anesthetized infants, the incidence of responsive cells was very low (10%, below four months) relative to that in awake behaving infants or in anesthetized or awake older ones (over 85%). This lack of responsiveness in anesthetized infant was specific to IT cortex; it was not found for either striate or MT cells.

Although the stimulus selectivity of IT neurons in unanesthetized infants appeared the same as in adults, the greater sensitivity of IT cortex to nitrous oxide in

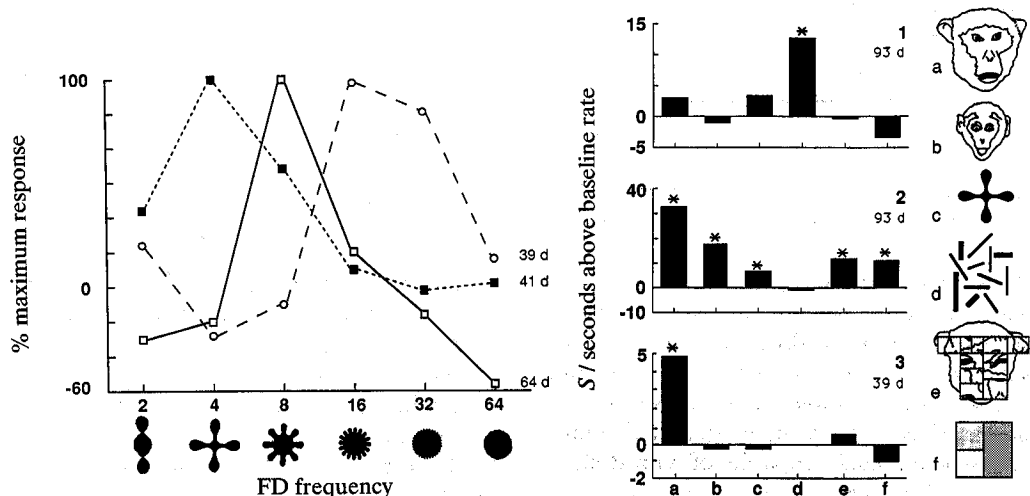


Figure 3. Responses of IT neurons in alert infant monkeys to the shapes illustrated. Zero on the left ordinate is spontaneous activity level. Age in days (d) at which each cell was recorded is indicated. Stimuli were black and white except for a, b, e and f. Each point or bar is an average of ten responses. Asterisks indicate statistically significant responses. (After Rodman *et al.* 1991.)

animals below four months suggests that some maturational process is taking place in IT cortex at about this age. This change in the effect of nitrous oxide may reflect some change in the synaptic or metabolic properties of IT neurons that is related to the anatomical and cognitive changes that are known to occur at this time (see references in Rodman *et al.* (1991)).

Further research is required to assess the role of experience in the first six weeks in maintaining and fine tuning whatever stimulus selectivity of IT neurons may be present at birth. However, given the existence of neonatal face recognition in humans, the existence of IT neurons with face and other complex selectivities near birth should not be surprising, assuming, of course, that they are required for face recognition.

5. SOME UNSOLVED PROBLEMS

The available evidence indicates that IT cortex represents the facial image in the same way that it represents all other visual experience, past and present, namely by means of some form of ensemble coding. Because faces are so important for monkeys, because faces are extraordinarily similar to each other, and because the ability to discriminate and remember faces is prodigious, ensembles for coding faces may have to be made up of relatively selective individual neurons, namely, ones that fire best to face-like stimuli. Of course, we have not solved the problem of face processing by simply conflating it to the problem of visual pattern processing. Here are some of the remaining questions about visual processing by IT cortex.

1. What is the nature of the ensemble code in IT cortex for visual stimuli? How many cells are involved in an ensemble and how are different ensembles specialized and spatially arranged?
2. Is the frequency of firing the only way that IT cells convey information or does the time structure of the response convey information, such as in a temporal pattern (Richmond *et al.* 1987), oscillation (Gray *et al.* 1990) or coordination of discharge among neurons (Gochin *et al.* 1991)?
3. Are the same IT cells involved in processing, holding in short-term store, permanently storing, and imaging visual stimuli?
4. Are the interactions between ventrolateral frontal cortex and IT cortex involved in some visual short-term or other memory process?
5. How do the interactions of IT cortex and limbic areas result in long term storage of visual information?
6. Can lesions or disconnections of specific regions of IT cortex result in prosopagnosia as well as other category specific agnosias?
7. What is the circuitry underlying the invariance of the response of many IT cells to change in stimulus size, location, and contrast? (see Gochin & Lubin 1990.)
8. Does the pulvinar modulate IT responsiveness and how does this modulation underlie attention?
9. What is the functional significance of the different cytoarchitecture, different connections, and vary-

ing receptive field size in different regions of IT cortex?

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Discussion

S. DE SCHONEN (*Cognitive Neuroscience Unit, L.N.F.1, C.N.R.S., Marseille, France*). At the age of 5 weeks, the number of synapses in the monkey's cerebral cortex has not yet decreased to the adult level (according to Rakic *et al.* (1986)). Does Professor Gross find that cells responding to faces are present in a larger region than in adult monkeys or in surrounding regions where they are not found in adult monkeys?

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C. G. Gross. The stimulus properties of inferior temporal neurons, including selectivity for faces, were similar in infant and adult animals. We did not sample sufficiently, however, to determine whether the spatial distribution of face-selective cells was similar in infants and adults.