Mechanisms of visual object recognition: monkey and human studies

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The feature-based representations of object images in the inferotemporal cortex of macaque monkeys have been further characterized by optical imaging experiments. Recently, the close correlation between the activity of inferotemporal cells and the perception of object images has been revealed by single-unit recordings from behaving monkeys. The human homologue of the monkey inferotemporal cortex has been identified through use of new non-invasive techniques.

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Abbreviations

fMRI	functional magnetic resonance imaging
PET	positron emission tomography
TE	inferotemporal cortex
V1	primary visual cortex

Introduction

Visual object recognition is a key function of the primate brain. It tolerates considerable changes in images, such as those caused by variable illumination and by different viewing angles and articulations of the object; it also is capable of automatic generalizations. The neural mechanisms of visual object recognition have been investigated both in behavioral studies of brain-damaged patients and monkeys with experimental lesions and in anatomical connection and unit-recording studies in monkeys. The recent development of non-invasive measurement techniques for examining the human brain has provided new and powerful tools, which have increased the speed of exploration. Here, I review the frontiers of research in this field, beginning with monkey studies and then going on to human studies.

The ventral visual pathway

The importance of the inferotemporal cortex (TE) for visual object recognition has been known for many years as a result of lesion studies in the monkey. Ungerleider and Mishkin [1] delineated the functional dichotomy between the serial cortical pathway leading from the primary visual cortex (V1) to TE and the pathway leading from V1 to the parietal cortex. The former was named the ventral visual pathway, and the latter the dorsal visual pathway. They labeled the function disrupted by lesions of the parietal cortex 'spatial vision'. Goodale and Milner [2] have recently insisted that the functions degraded by damage to the parietal cortex are better summarized as 'visual control of action' rather than 'spatial vision'. However, these views are not mutually inconsistent. The spatial relations between objects and those between objects and the actor are the most important parameters for the control of action.

The ventral visual pathway goes from V1, through V2, V4, TEO (or PIT: posterior TE), to TE. The step-by-step projections are the strongest, but there are also connections that jump one step, such as those from V2 to TEO and those from V4 to TE. Not only do lesions of TE disrupt object recognition, but so do complete lesions of the intermediate stages along this pathway [3]. The retinotopic organization becomes coarser along the pathway, and no sign of retinotopic organization has been reported in TE. Among the projection sites from TE, the perirhinal cortex (Brodmann's areas 35 and 36) and the upper bank of the anterior superior temporal sulcus are dominantly visual. In this respect, TE does not represent the final stage of the ventral visual pathway.

Feature-based representation

In the early 1980s, Bruce *et al.* [4] and Perrett *et al.* [5] identified a group of cells in the depth of the superior temporal sulcus that responded selectively to the visual presentation of faces compared to non-face objects. These 'face' cells required all the essential features of a face for maximal activation. The existence of cells specific for the representation of faces cannot be generalized, however, to cells specific for the representation of non-face objects.

My group has developed a reduction method to study the stimulus selectivity of inferotemporal cells in monkeys (reviewed in [6•]). After we isolated the activity of a single cell, we manually presented the monkey with dozens of three-dimensional objects, including animal and plant imitations, so as to identify effective stimuli. We then recorded the images of the effective stimuli using a video camera. The images were stored on a computer and could be displayed on a television screen. We then determined the most effective stimulus for each cell being recorded. The image of the most effective stimulus was then simplified step by step on the computer whilst maintaining maximal activation. The simplest image that could still elicit maximal activation from the recorded neuron was designated the critical feature for that cell.

The critical features for the activation of cells in TE are moderately complex. They are more complex than orientation, size, color, and simple texture, which are known to be extracted and represented by the activity of

cells in V1. At the same time, however, the critical features are not specific enough to represent the natural objects through the activity of a single cell—a combination of several to several tens of cells is needed. Faces are the exceptions. For many of the face cells, the image of the face cannot be simplified very much without losing maximal activation. Applying the reduction method to the intermediate stages along the ventral pathway, Kobatake and Tanaka [7] found that cells that require complex features for maximal activation can be found as early as V4; however, the proportion of such cells increases, and their tuning becomes sharper, in TE.

By making long vertical and oblique penetrations and by comparing the stimulus selectivity of many cells recorded along the long penetrations, Fujita *et al.* [8] found that cells with similar selectivity cluster in columnar regions in TE. In vertical penetrations, cells recorded throughout the whole thickness of the gray matter responded to similar features. In the oblique penetrations, however, cells with selectivity similar to the first cell's selectivity were limited to a short span whose projection onto the cortical surface was, on average, 400 microns. It was thus suggested that TE is composed of columnar modules, each containing cells that respond to similar features.

Continuous mapping of features

Wang *et al.* [9••] used optical imaging of intrinsic signals to study further the spatial properties of the columnar organization in TE: they exposed the cortical surface, illuminated it with red light tuned to 605 nm, and then recorded the reflected image using a CCD video camera. The reflected images were compared with those obtained using different visual stimuli and with the image obtained by presentation of a blank screen. Before doing this, however, Wang *et al.* [9••] first recorded the responses of single cells using a microelectrode in order to determine their critical features. While the monkey looked at the critical feature, an activation spot appeared around the penetration site at which the critical feature had been determined for a single cell. No activation spot was observed at the same location when the monkey looked at simpler features. Although the critical feature of only a single cell was determined, it is likely that a large proportion of cells in the region are activated to produce the observed metabolic change. This implies that the localized and specific occurrence of activation spots represents a regional clustering of cells with similar stimulus selectivity.

This optical imaging experiment not only confirmed the regional clustering of cells with similar selectivity, but also revealed an interesting property of TE columnar organization: namely, the overlap of columns activated by different but related features. The most impressive data were obtained using faces from different view angles.

Motivated by the intermingled recordings of three cells maximally responding to a frontal face view and two cells maximally responding to a profile (lateral view) within one electrode penetration, Wang *et al.* [9••] presented five different perspectives of the same doll's face during the optical imaging session. All the different perspectives evoked activation spots around the penetration site. The spots overlapped, but their centers differed slightly, so that the activation spot moved around as the face rotated from the left profile to the frontal view, and then to the right profile. Individual spots measured 300 μm to 400 μm in diameter, and the overall region over which their centers moved had a long axis of 800 μm. These regions were not activated by the non-face stimuli tested during optical imaging.

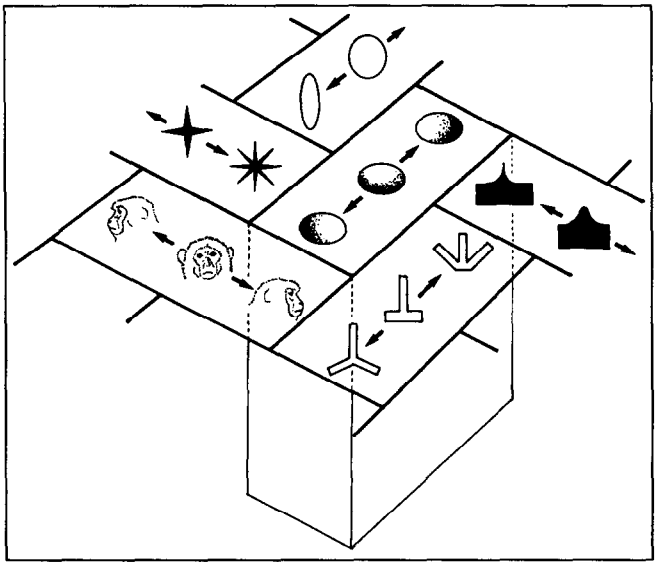
Similar results, namely selective activation by faces and a systematic shift in the activation spot with the rotation of the face, were obtained in three other monkeys [9••]. In these three monkeys, optical imaging was not guided by the unit recording. The recording chamber (with an inner diameter of 18 mm) was placed in the same part of TE as described above, and face-selective activation was found at roughly the same location (approximately the posterior third of TE, on the lateral surface close to the lip of the superior temporal sulcus). The effects of rotating the face around a different axis and of changing the facial expression were also tested, but neither of these caused a shift in the activation spot. Only two faces were tested: a human face and a doll's face. Both the human face and the doll's face activated mostly overlapping regions. There are two possible interpretations for this result. One is that the variations other than those with horizontal rotation are represented at different sites not covered by the recording chamber in the experiments. Alternatively, it is possible that only the variations along the horizontal rotation are explicitly mapped as the first principal component, and other variations are imbedded in overlapping cell populations.

The data for non-face features are more limited, but I hypothesize that there exist similar continuous maps for non-face features (see [6•]) (Figure 1). One function of the inferotemporal columns may be to augment feature variations around selected center points in the feature space; they may also facilitate computations among these variations. One or two principal components of these variations are mapped along the cortical surface.

Close correlation between inferotemporal cell activity and perception

Evidence showing that responses of single cells in the monkey TE correlate well with overall perception has accumulated. Ito *et al.* [10] examined the effect of size changes on responses, and found that a group of inferotemporal cells responded to particular shapes over 64-fold size differences. Sary *et al.* [11] found that the shape selectivity of inferotemporal cells in unanesthetized monkeys does not vary with the size and position of a

Figure 1



Schematic diagram of the columnar organization in the monkey inferotemporal cortex. Columns representing different but related features overlap with each other and form a continuous map of features. Adapted from [6•].

shape and also does not vary with the visual cue used to define the shape. This cue invariance extended to static luminance and texture cues, as well as to relative motion cues.

Kovacs *et al.* [12] examined whether inferotemporal cells respond to objects despite the presence of a foreground occluder. In certain conditions, the foreground occluder does not interfere with the perception of objects by humans [12]. Correspondingly, the monkey inferotemporal cells maintained their selectivity for shapes in the presence of occluding foreground objects, although their response magnitude decreased. The correlation breaks for effects of the closure of the occluding object contours. Human perception of occluded objects is much easier when the contours of the occluding object are closed, such that the occluder is entirely visible. However, the responses and selectivity of monkey inferotemporal cells were equally good whether or not the occluding object was closed. This discrepancy may represent either a difference between the human and monkey perception or a difference between the perception and the inferotemporal cells' responses.

An image approaches dual tonality when it is illuminated in such a way as to cast strong shadows. In two-tone pictures, it becomes extremely difficult to perceive the image of an object if there are contours in the background continuous with the outer contours of the object. If a subject looks at a gray-scale image of the same scene, however, perception of the two-tone image becomes much easier thereafter. Tovee *et al.* [13••] found that monkey inferotemporal cells respond in a parallel manner. They recorded cells responding to faces. Responses of inferotemporal cells to the two-tone image containing a face increased considerably after exposure to the gray-scale version of the same picture. Tovee *et al.* [13••] interpreted this result as rapid learning by inferotemporal cells. The result could also be interpreted as the effect of feedback from limbic structures or the prefrontal cortex, which may hold some trace of the interpreted gray-scale image.

Logothetis's group [14•,15••] has made remarkable findings using the technique of binocular rivalry. When different images are presented to the left and right eyes, a subject does not perceive a combination of the two images, but rather each image alternately. By presenting a stimulus that evoked strong responses from a recorded cell to one eye, and a null stimulus to the other eye, Logothetis and co-workers [14•,15••] compared the responses of inferotemporal cells with the monkey's reported perception. The monkey had been trained to make differential reports according to two predetermined stimulus categories. Faces were used in the experiments with inferotemporal cells. Only 18% of the cells in V1 responded consistently with the monkey's report. This proportion increased to 25% in V4 [14•], and nearly all the inferotemporal cells responded consistently with the monkey's perception [15••]. These results indicate that the conscious perception of objects is better correlated with cell activities in TE than in earlier visual cortices. This finding is also consistent with the recent proposition by Crick and Koch [16] that consciousness is situated in anterior regions of the brain.

The interaction between TE and the perirhinal cortex

The importance of the perirhinal cortex for the association of different visual features has been suggested by the results of several lesion studies in the monkey [17–19]. A series of studies by Miyashita's group (see [20,21••]) has shown that feedback from the perirhinal cortex is crucial for the responses made by inferotemporal cells to very complex stimuli. The task paradigm they used was associative pair matching. The stimuli were composites of Fourier descriptor figures. They made 12 arbitrary pairs of stimuli; the monkeys had to select the corresponding member of a pair when cued by the other member of the pair. After about a month of training, association was established at the behavioral level, and inferotemporal cells were recorded. Some cells responded to both stimuli composing a pair, and this pairing was shown to be significantly more frequent than that expected by chance [20].

Higuchi and Miyashita [21••] taught the same task to other monkeys, which subsequently received anterior commisurotomies. After association was established (see above), they neurochemically lesioned the perirhinal and entorhinal cortices in one hemisphere. At the behavioral level, the association remained intact because of the intact hemisphere, but none of the inferotemporal cells on the

lesioned side responded to the two stimuli composing the pairs. Because the responses to the individual stimuli were normal, the feedback from the perirhinal and entorhinal cortices was deemed essential only for the association of the paired stimuli.

Saleem and Tanaka [22•] injected phaseolus lectin (PHA-L) into a focal region (<1 mm diameter) in TE and examined the distribution of labeled terminals in the perirhinal cortex. After an injection into the ventral part of anterior TE, labeled terminals were found to be widely distributed, covering more than half the total extent of the perirhinal cortex. Together with the retrograde tracer studies of Suzuki and Amaral [23], this study showed that the projections from ventral TE to the perirhinal cortex have both considerable divergence and convergence. These highly divergent and convergent connections probably underlie the role of the perirhinal cortex in stimulus–stimulus associations.

PET and fMRI studies of human TE

Overall, the functional map of the brain is preserved from the monkey to the human. Human V1 is located in the occipital pole, as it is in the monkey. Damage to the inferior temporal cortex in humans produces deficits different from those caused by damage to the parietal cortex, in a manner consistent with the ventral versus dorsal functional dichotomy established in the monkey. However, because language-related regions have evolved in the human temporal cortex, we cannot match point-by-point the human inferior temporal cortex to that of the monkey. Neuropsychological studies of brain-damaged patients have suggested that the anterior part of the inferior temporal cortex works as an interface between visual images and the lexical representation of objects [24••]. To understand the process of visual object recognition in the human brain, we need to know the location and extent of the human homologue of monkey TE.

A series of PET studies by Haxby and Ungerleider's group [25,26] has demonstrated the distinction between the object identification pathway and the object location pathway. In their studies, the same stimuli composed of one sample face and two 'choice' faces were used in two different tasks. In the face-identification task, the subjects had to indicate which of the two choice faces matched the sample face. In the location task, the subjects had to match the position of the face relative to the side of the display box marked by a double bar. When compared to the activation produced by a sensory–motor control task using scrambled images, the face-identification task and the location task evoked activation over large posterior brain regions, with an extensive overlap centered on the occipital pole. When compared to each other, however, specific activations were split into the ventral and dorsal regions. The activation specific to the face-identification task was distributed along the ventral surface of the occipital cortex and the posterior part of the temporal cortex. Kohler *et al.* [27], using a similar task design but with non-face objects, obtained similar results.

The functional magnetic resonance imaging (fMRI) studies of Sereno *et al.* [28], Tootell *et al.* [29], and DeYoe *et al.* [30] have demonstrated that occipital regions surrounding V1 are arranged in retinotopically organized areas that can be activated by simple stimuli. In accordance with the retinotopic arrangements in the monkey brain, they designated these regions as the human homologues of V2, V3, V3a, and V4. Malach *et al.* [31] proposed a region near the occipital and temporal border as a candidate for the homologue of monkey TE. Using both simple and complex images, they compared the activity in the retinotopically organized occipital regions with that in more anterior regions. Pictures of objects as well as their scrambled images evoked comparably strong activation in V1; however, the object pictures activated a region at the occipital and temporal border much more strongly than the scrambled images. They named this area the LO complex. Kushnir *et al.* [32] reported that LO does not have left–right retinotopic organization. Hence, this area is most probably a part of the human homologue of monkey TE.

Kanwisher *et al.* [33•] have conducted a PET experiment using a similar paradigm, and obtained a similar result: a localized area near the occipital and temporal border was significantly more activated by images of objects than scrambled images. But, this activation area was a little more anterior and ventral than LO. However, LO and the area found by Kanwisher *et al.* [33•] have a common characteristic: generality across objects. Both faces and non-face objects evoked comparably strong activations, as did familiar and novel objects.

Moving in the anterior direction towards the middle part of inferior temporal cortex, the activation becomes more stimulus selective. McCarthy's group [34–36] has studied activation by faces in the fusiform gyrus, first making local EEG recordings using chronically implanted subdural electrodes in epilepsy patients [34], and then using fMRI on normal subjects [35,36]. They distinguished activation by faces from activation by scrambled faces, textures, and non-word letter strings. Face activations were found bilaterally in the fusiform gyrus, but letter string activations were found more laterally in the occipito-temporal sulcus of the left hemisphere only.

Kanwisher *et al.* [37,38••] compared activation by faces with that by non-face objects. Voxels that were significantly more activated by non-face objects than faces were located bilaterally in the fusiform gyrus and parahippocampal gyrus, but voxels significantly more activated by faces than objects were located more anteriorly in the fusiform gyrus and only in the right hemisphere in most subjects.

McCarthy *et al.* [39••], using a kind of masking method, distinguished face-specific activation from activation by objects in general. Their results were similar to those of Kanwisher *et al.* [37,38••], but the activation area was even smaller (on average 280 mm^3). Although the specificity of the activation by letter strings has not been tested further, the specific activations are in line with the existence of pure alexia, that is, specific deficits in reading found in certain brain-damaged patients [40,41]. These middle parts of the ventral surface of the temporal cortex may also be a part of the human homologue of the monkey TE. A subsystem specific to faces is known to have developed in the monkey TE, but it may well be that one specific to letter strings has developed in the human TE. Differential activations have also been observed in the inferior temporal cortex with the task of naming visually presented objects [25,42,43].

Imaging columns by fMRI

The goals of cognitive brain science are not only functional localization, but also the elucidation of the computational algorithms that underlie the localized functions. In order to study the computational algorithms, the representational scheme for relevant information must be clarified. Representational schemes may be studied by examining the functional microstructures within the activations shown by PET and fMRI. Yang *et al.* [44•] used fMRI at 7 Tesla to study the activation of a single whisker barrel in rat cortex. The slice thickness was 1 mm and the in-plane resolution was 0.2 mm. A single whisker was vibrated and the image during stimulation was compared with the image without stimulation. A single narrow columnar region within the gray matter was activated. Different non-overlapping regions were activated by the stimulation of different whiskers. Woolsey *et al.* [45], using different, invasive methods, showed that the arterioles and venules that vertically penetrate the gray matter from the cortical surface do not have column specification — that is, the perfusion area of a single arteriole or venule covers several whisker barrel columns. Therefore, the result of Yang *et al.* [44•] also suggests the presence of flow regulation at the capillary level.

In the monkey and cat brain, it has been established that regions of cells receiving dominant inputs from either the left or right eye are alternately arranged in V1. Using fMRI, Menon *et al.* [46••] have succeeded in resolving the ocular dominance columns in human V1. They used a single flashing LED (light-emitting diode), one for each eye. When the flashing LED was presented alternately to the left and right eyes and the signal levels were compared between the two periods, significant activations were localized to small patchy regions. Confined to the gray matter, the patches measured about 1 mm, and the spacing between the patches was also about 1 mm. Horton and Hocking [47] stained V1 for cytochrome oxidase in a deceased patient who had lost input from one eye late in life. They drew the conclusion that the width of the ocular dominance columns in human V1 is about 1 mm. Therefore, the patches that Menon *et al.* [46••] observed in the differential fMRI images probably represented the ocular dominance columns.

Studies in monkey TE have demonstrated the columnar clustering of cells with similar stimulus selectivity. This means that the activation of cortical patches of column size is closely related to the activation of single cells. If the spatial resolution of fMRI were increased to the level of the column, we would be able to examine the representation of information, and the study of the neural mechanisms of visual object recognition would be further accelerated.

Conclusions

The representation of object images in TE of the monkey temporal lobe is based on features that are moderately complex. Variations in features are represented by cells in specific columns and their neighbors. The spread, transfer, and competition of activation may take place in local networks composed of these cells, acting on inputs provided by either feedforward (in perception) or feedback (in imagination) pathways. Each set of overlapping columns are commonly used by multiple classes of objects. Modules that are specialized for different individual classes of objects do not exist, with the exception of faces, for which there are specialized columns. Translation of face images for rotation, illumination changes, and expression changes may take place within these columns so as to assist identification of faces: for example, as an activation spot moves along the continuous map, the represented face image changes from a front view to a profile.

The ventral surface of the human brain, extending from around the occipito-temporal border to the middle part of the temporal cortex, has been designated as the human homologue of the monkey TE. Insofar as the activations have been examined with a spatial resolution of 1 mm, the regions situated around the occipito-temporal border are generally activated by complex object images without selectivity to a particular class of objects or a dependency on familiarity. In the middle part of the temporal cortex, some regions are activated more significantly by faces whereas other regions are more activated by non-face objects. The presence of regions activated specifically by letter strings has also been suggested [36]. Such modularity has probably evolved as a result of the differential characteristics of visual images of different object classes or the differential associations formed by their visual images with information represented at other brain sites: for example, faces are associated with information in the amygdala but letter strings are associated with information in the parietal cortex. Observations with column-level spatial resolution are needed to infer the representation schemes of these regions.

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