

INFEROTEMPORAL CORTEX AND OBJECT VISION

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ABSTRACT

Cells in area TE of the inferotemporal cortex of the monkey brain selectively respond to various moderately complex object features, and those that cluster in a columnar region that runs perpendicular to the cortical surface respond to similar features. Although cells within a column respond to similar features, their selectivity is not necessarily identical. The data of optical imaging in TE have suggested that the borders between neighboring columns are not discrete; a continuous mapping of complex feature space within a larger region contains several partially overlapped columns. This continuous mapping may be used for various computations, such as production of the image of the object at different viewing angles, illumination conditions, and articulation poses.

Introduction

Recognizing objects by their visual images is a key function of the primate brain. This recognition is not a template matching between the input image and stored images but a flexible process in which considerable change in images—due to different illumination, viewing angle, and articulation of the object—can be tolerated. In addition, our visual system can deal with images of novel objects, based on previous visual experience of similar objects. Generalization may be an intrinsic property of the primate visual system. In this article, I discuss the neural organization essential for these flexible aspects of visual object recognition in the anterior part of the inferotemporal cortex.

The inferotemporal cortex (IT) of the monkey brain has been divided into subregions in several different manners. Our own division into posterior IT and anterior IT, based on the size of the receptive fields and the properties of responses (Tanaka et al 1991, Kobatake & Tanaka 1994), roughly corresponds to the previous cytoarchitectural division into TEO and TE (Iwai & Mishkin 1967; von Bonin & Bailey 1947, 1950): Posterior IT corresponds to TEO, and

anterior IT to TE. I use TEO and TE in this article because they are more popular.

TE receives visual information from the primary visual cortex (V1) through a serial pathway, which is called the ventral visual pathway (V1-V2-V4-TEO-TE). Although there are also jumping projections, such as that from V2 to TEO (Nakamura et al 1993) and that from V4 to the posterior part of TE (Saleem et al 1992), the step-by-step projections are more numerous. The IT projects to various brain sites outside the visual cortex, including the perirhinal cortex (areas 35 and 36), the prefrontal cortex, the amygdala, and the striatum of the basal ganglia. The projections to these targets are more numerous from TE, especially from the anterior part of TE, than from the areas at earlier stages (Iwai & Yukie 1987, Ungerleider et al 1989, Saleem et al 1993a, Cheng et al 1993, Suzuki & Amaral 1994). Therefore, there is a sequential cortical pathway from V1 to TE, and outputs from the pathway originate mainly in TE.

Monkeys that have had their TE bilaterally ablated showed severe but selective deficits in learning tasks that required the visual recognition of objects (Gross 1973, Dean 1976). These behavioral results, together with the above-described important anatomical position of TE, suggest that TE is the site of neural organization essential for the flexible properties of visual object recognition.

In this review, our own data are emphasized, and the citation of other references is selective. This selection is not based only on the value of the studies but also on their relevance to the subject. The readers should read other reviews to get an overview of studies in the IT, e.g. Rolls (1991), Miyashita (1993), Gross (1994), and Desimone et al (1994). In particular, mechanisms of short-term memory of object images are not discussed in this article. I first summarize the data from unit-recording experiments to show that cells in TE respond to moderately complex object features and that those that cluster in a columnar region respond to similar features. I then consider the process by which the selectivity is formed in the afferent pathways to TE. I introduce the data of optical imaging of TE in order to discuss the function of the TE columns. Finally, I consider how the concept of the object emerges in the brain. The selections of our recordings that are introduced in this article were all conducted in anesthetized preparation, and they were from the lateral part of TE, lateral to the anterior middle temporal sulcus (AMTS). This part is often referred to as TEd (dorsal part of TE).

Stimulus Selectivity of Cells in TE

One obstacle in the study of neuronal mechanisms of object vision has been the difficulty in determining the stimulus selectivity of individual cells. There

is a great variety of object features in the natural world, and we do not know how the brain scales down the dimension of this variety.

Single-unit recordings from TE were initiated by Gross and his colleagues (Gross et al 1969, 1972). They found that cells in TE had large receptive fields, most of which included the fovea, and that some cells responded specifically to a brush-like shape with many protrusions or to the silhouette of a hand. They extended the study of the stimulus selectivity by using two different methods: a constructive method and a reductive one. In the constructive method, they used Fourier descriptors that were defined by the number (frequency) and amplitude of periodic protrusions from a circle. Any contour shape can be reconstructed by linearly combining elementary Fourier descriptors of single frequency and amplitude. Some cells responded specifically to Fourier descriptors of a particular range of frequencies, with a considerable invariance for the overall size of the stimulus (Schwartz et al 1983). This method was not very promising, however, because the same group of authors found that the response of a TE cell to a composite contour was far from the linear combination of its responses to the elementary component contours (Albright & Gross 1990). Fourier descriptors are not the basis functions that the IT uses for the representation of object images.

The other direction that Gross's group pursued was reductive. They first presented many object stimuli for individual cells in order to find effective stimuli. Next, the images of the effective stimuli were simulated by paper cutouts to determine which features were critical for the activation (Desimone et al 1984).

We expanded this latter method and have developed a systematic reduction method with the aid of a specially designed image-processing computer system (Tanaka et al 1991; Fujita et al 1992; Kobatake & Tanaka 1994; Ito et al 1994, 1995). After spike activities from a single cell were isolated, many three-dimensional (3D) animal and plant imitations were presented to find the effective stimuli. Different aspects of the objects were presented with different orientations. Next, the images of the effective stimuli were recorded with a video camera and presented on a TV monitor by the computer to determine the most effective stimulus. Finally, to determine which feature or combination of features contained in the image was essential for the maximal activation, the image of the most effective object stimulus was simplified step-by-step while the activity of the cell was monitored. The minimal combination of features that evoked the maximal activation was determined as the critical feature for the cell. Figure 1 exemplifies the process for a cell for which the effective stimulus was reduced from the view of a water bottle to a combination of a vertical ellipse and a downward projection from the ellipse.

After the reduction was completed, the image was modified so that the selectivity could be further examined. Figure 2 exemplifies this latter process

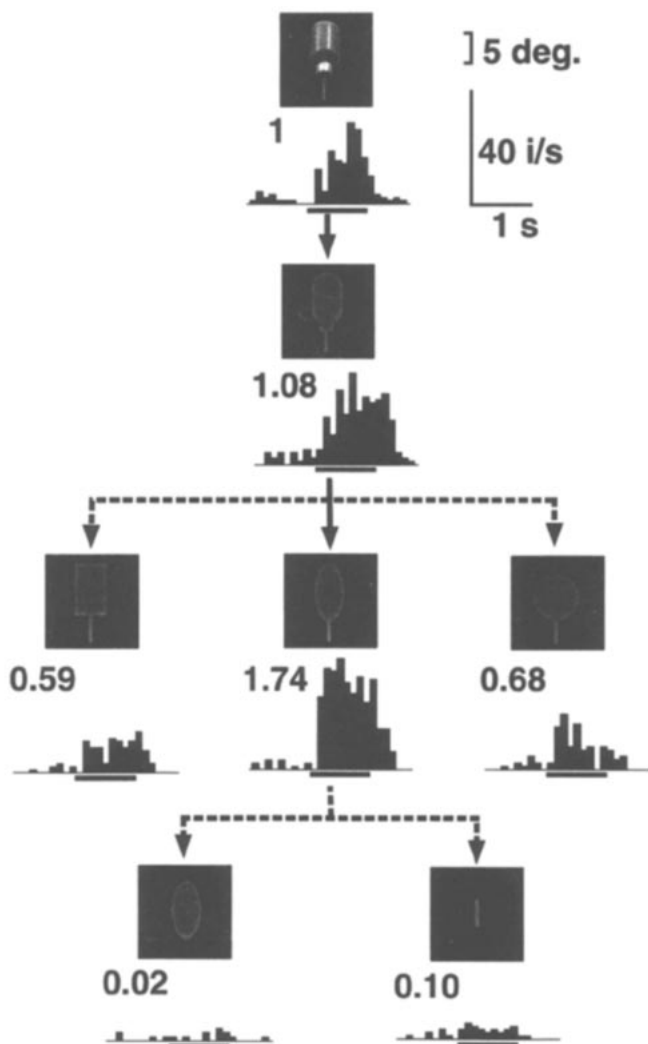


Figure 1 An example of the reduction process to determine the feature critical for the activation of cells in the ventral visual pathway. The responses were averaged over ten repetitions of the stimuli. The underlines indicate the period of stimulus presentation, and the numbers above histograms indicate the magnitude of the responses normalized by the response to the image of a water bottle.

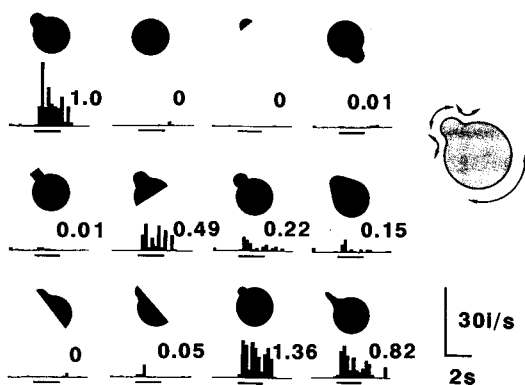


Figure 2 An example of further study of the selectivity after the reduction process was completed. This cell was recorded from TE.

for a cell, which is one of the cases in which the domain of selectivity was most clearly determined. The cell responded maximally to a pear model within the routine set of object stimuli, and the critical feature was determined as a rounded protrusion in the 10 o'clock direction from a rounded body with a concave smooth neck. The body or the head by itself did not evoke any responses (the first line in Figure 2). The head had to be rounded because the response disappeared when the rounded head was replaced by a square, and the body had to be rounded because the response decreased by 51% when the body was cut in half (the second line, left). The neck had to be smooth and concave because the response decreased by 78 or 85% when the neck had sharp corners or was straight (the second line, right). The critical feature was neither the right upper contour alone nor the left lower contour alone, because either half of the stimulus did not evoke responses (the third line, left). The width and length of the projection were not very critical (the third line, right).

By determining the critical features for hundreds of cells in TEd, we concluded that most cells in TEd required moderately complex features for their activation, e.g. the 16 examples in Figure 3. The critical features were more complex than orientation, size, color, and simple texture, which are known to be extracted and represented by cells in V1. Some of the features were moderately complex shapes, while others were combinations of such shapes with color or texture. Responses were selective for the contrast polarity of the shapes: The contrast reversal of the critical feature reduced the response by >50% in 60% of tested cells, and replacement of the solid critical features by

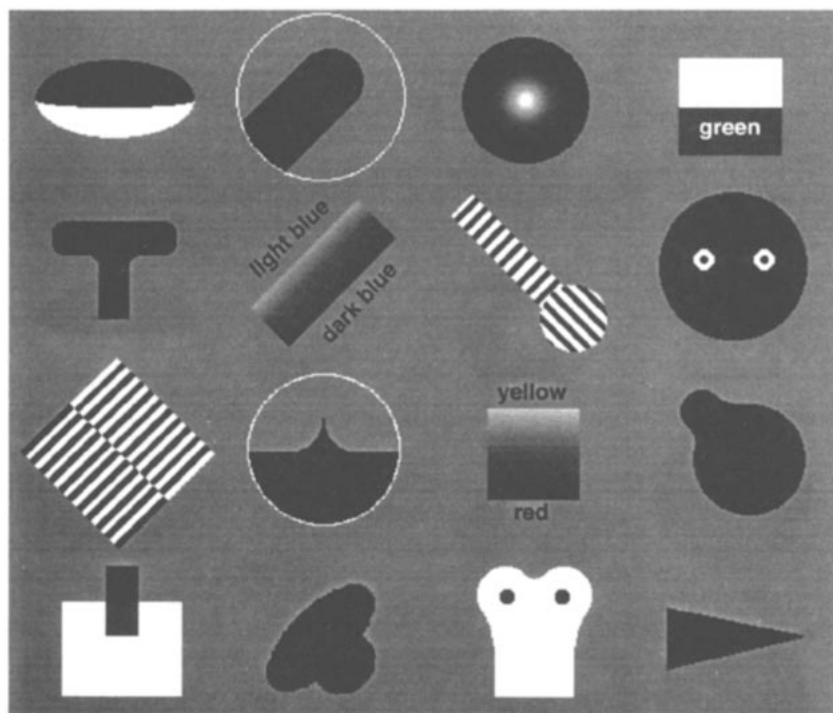


Figure 3 Sixteen examples of the critical features of cells in TE. They are moderately complex.

line drawings of the contour reduced the response by >50% in 70% of tested cells (Ito et al 1994).

Invariance or Selectivity for Position, Orientation, and Size

Gross et al (1972), in their pioneering experiments, found that cells in TE_d had large receptive fields across which a stimulus kept evoking responses. By using a set of shape stimuli composed of the critical feature independently determined for individual cells by the reduction method and several other shape stimuli made by modifying the critical feature, we demonstrated that the selectivity for shape was mostly preserved over the large receptive fields (Ito et al 1995). In contrast, responses of TE_d cells to their critical features were more selective for the orientation in the frontoparallel plane (Tanaka et al 1991) and for the size of the stimuli (Ito et al 1995).

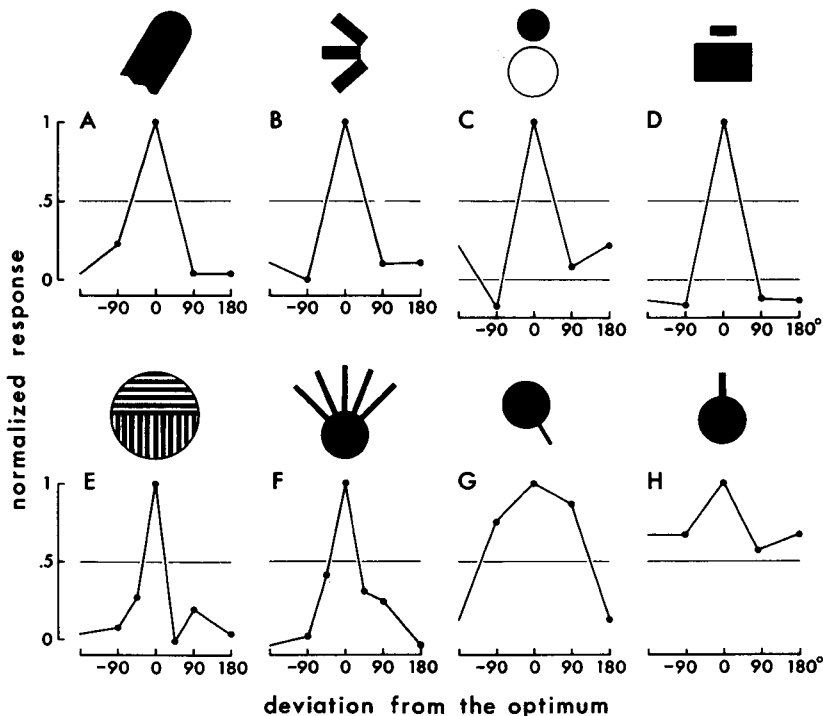


Figure 4 Tuning of responses of eight TE cells for the orientation of stimulus.

Figure 4 shows the data of eight cells for the tuning of responses for the orientation in the frontoparallel plane. The eight cells were selected so that they represent the general properties of cells in TEd. Rotation of the critical feature by 90° decreased the response by $>50\%$ for most cells (Figure 4A–F). The tuning of the remaining cells was broader: The response was reduced by $>50\%$ by a rotation of 180° (Figure 4G), or the cell showed $<50\%$ change (Figure 4H).

The effects of changes in stimulus size varied more among cells than did position or orientation. Twenty-one percent of TEd cells tested responded to size ranges of more than four octaves of the critical features, whereas 43% responded to size ranges of less than two octaves. Tuning curves of four TEd cells, two from each group, are shown in Figure 5. The tuned cells may be in the course of constructing the size-invariant responses, or alternatively, there are both size-dependent and -independent processing of images in TEd.

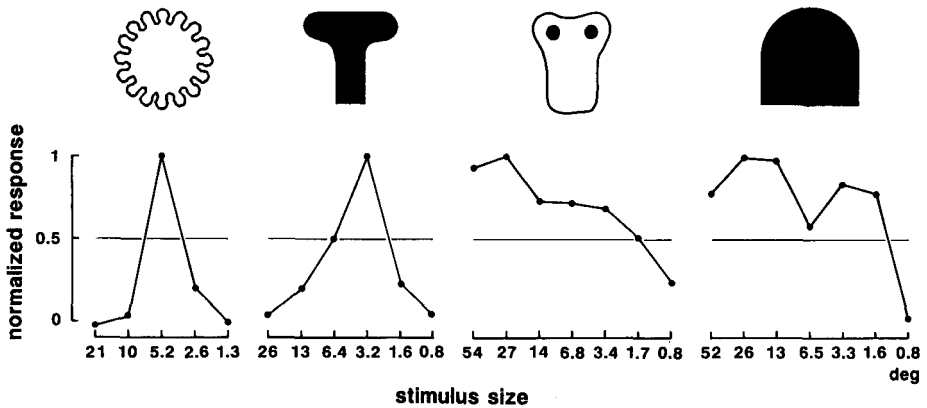


Figure 5 Tuning of responses of four TE cells for the size of stimulus.

Columnar Organization in TE

How are cells with various critical features distributed in TE? Is there a columnar organization like that found in V1? By simultaneously recording, with a single electrode, from two or more TE_d cells, we have found that cells located at nearby positions in the cortex have a similar stimulus selectivity (Fujita et al 1992). The critical feature of one isolated cell was determined by using the procedure described above, while responses of another isolated cell, or nonisolated multiunits, were simultaneously recorded. In most cases, the second cell responded to the optimal and suboptimal stimuli of the first cell. The selectivity of the two cells varied slightly, however, in that the maximal response was evoked by slightly different stimuli, or the mode of the decrease in response was different when the stimulus was changed from the optimal stimulus. Figure 6 shows an example of the latter case.

To determine the spatial extent of the clustering of cells with similar selectivity, we examined responses of cells recorded successively along long penetrations made perpendicular or oblique to the cortical surface (Fujita et al 1992). The critical feature of a cell located at the middle of the penetration was determined first. A set of stimuli, including the optimal feature for the first cell, its rotated versions, and ineffective control stimuli, were made, and cells recorded at different positions along the penetration were tested only with the fixed set of stimuli. As in the example shown in Figure 7, cells recorded along the perpendicular penetrations commonly responded to the critical feature of the first cell or some related stimuli. The span of the commonly responsive cells covered nearly the entire thickness from layer 2 to 6. The

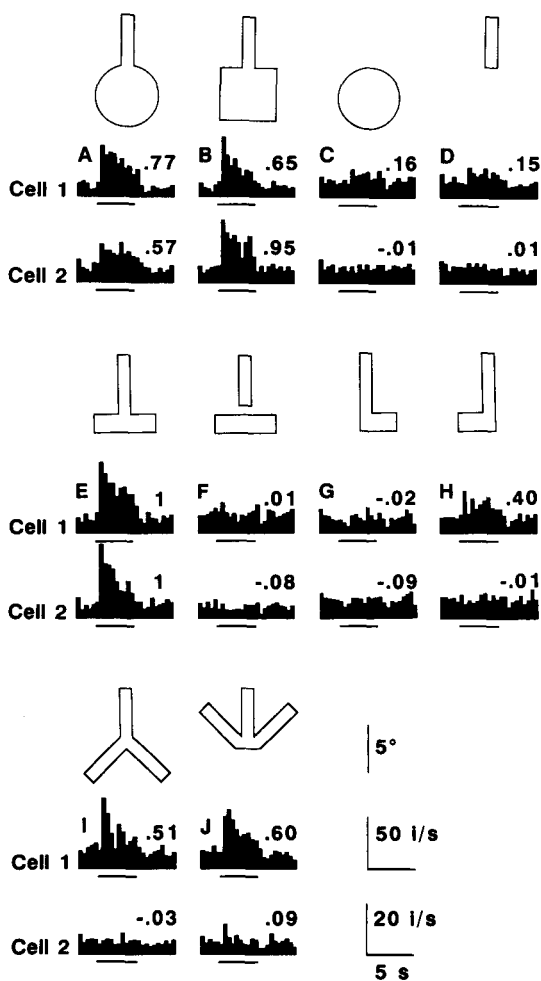


Figure 6 An example of simultaneous recording from two nearby neurons in TE.

situation was different in the penetrations made oblique to the cortical surface. The cells that were commonly responsive to the critical feature of the first cell or its related versions were limited to a short span around the first cell. The horizontal extent of the span averaged 400 μm . The cells outside the span either were not responsive to any of the stimuli included in the set or responded to some stimuli that were not effective for the first cell and were included in the set as ineffective control stimuli.

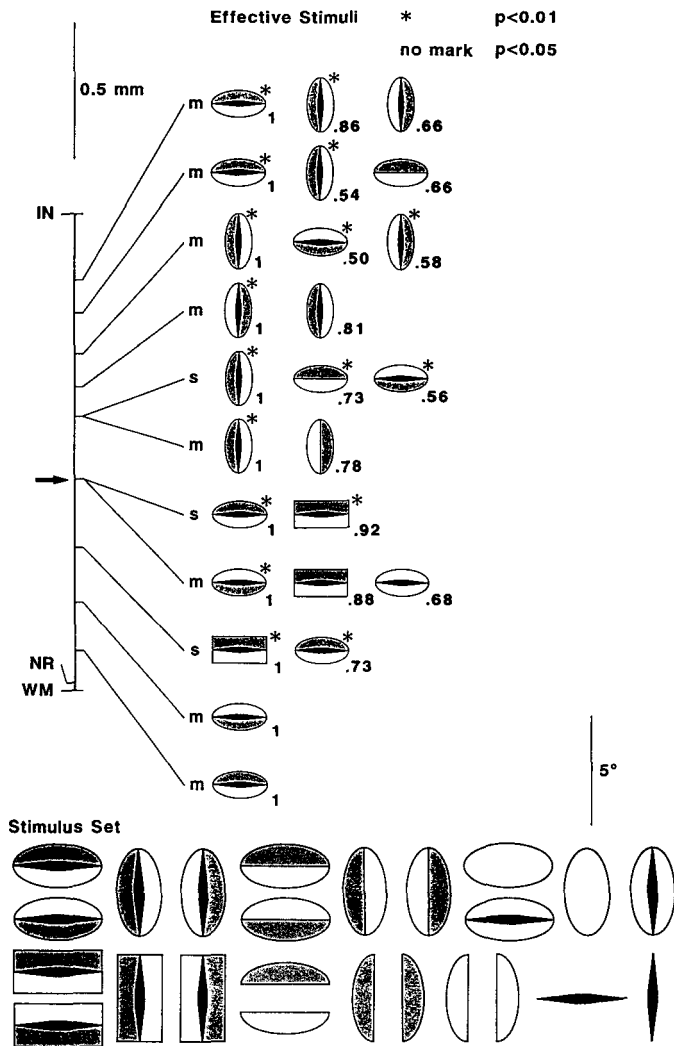


Figure 7 Responses of cells recorded along a perpendicular penetration in TE. The responsiveness of the cells was tested with the set of stimuli shown at the bottom, which were made in reference to the critical feature of the first cell indicated by the arrow. Effective stimuli are listed separately for individual recording sites, in the order of effectiveness. "m" indicates recording from multiunits, and "s" from single units.

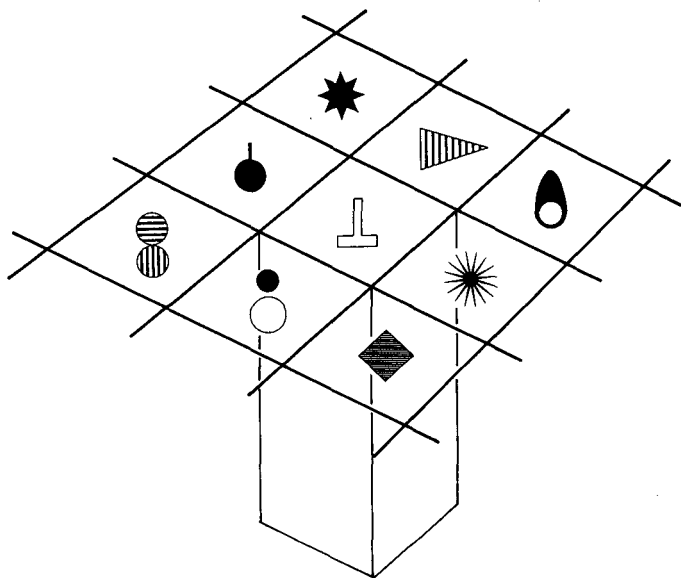


Figure 8 Schematic drawing of columnar organization in TE.

The TED region is thus composed of columnar modules in which cells respond to similar features (Figure 8). Cells within the same column respond to similar features, but cells in different columns respond to different features. The width of a columnar module across the cortical surface may be slightly greater than $400\ \mu\text{m}$. The span of a column along an oblique penetration should be smaller than the real size of the column if the penetration crosses its periphery. The number of modules, which was estimated by a division of the whole surface area of TEed into $500 \times 500\ \mu\text{m}$ squares, was 1300.

Organization of Afferents to TE

The selective responses to complex features, which were first found in TE cells, have been traced to earlier stages in the afferent pathway to TE. We have found that cells requiring such complex features for the maximal activation were already present in TEO and V4 (Kobatake & Tanaka 1994), although their proportion was small. Gallant et al (1993) also found that there were cells that responded preferentially to concentric or hyperbolic stripes rather than to straight stripes. The optimal features that we found in these areas were much more divergent, though they included concentric stripes.

To compare such cells in TEO and V4 with cells in TE, we compared

responses of individual cells to a fixed set of stimuli of simple features to their responses to individually determined critical features (Kobatake & Tanaka 1994). The set stimuli were composed of 16 bars of 4 different orientations with a 45° interval and 2 different sizes (0.5° by 10° and 0.5° by 2°) and 16 colored squares of 4 different colors and 2 different sizes (0.5° by 0.5° and 2.5° by 2.5°). Stimuli both darker than and lighter than the background were included. This set evoked some good, though not maximal, responses in cells in V2 and V4 that showed selectivity only in the domain of orientation or color, and size. Either most cells in TE did not respond to the simple stimuli included in the set, or the responses were negligible compared with their responses to the individually determined complex critical features (Figure 9, *left*), whereas cells in TEO and V4 showed divergent properties in responses to the simple stimuli. Some TEO and V4 cells showed no or negligible responses to any of the simple stimuli as cells in TE; some others showed moderately strong responses to some of the simple stimuli in addition to the maximum response to the complex critical features (Figure 9, *right*); and the remaining cells even maximally responded to some of the simple stimuli. Figure 10 shows the proportion of three groups of cells that were classified by setting arbitrary borders at 0.25 and 0.75 in the magnitude of the maximum response to the simple stimuli normalized by the overall maximum response of the cell.

TEO and V4 were thus characterized by the mixture of cells with various levels of selectivity. We may take this mixture of various cells as evidence that selectivity is constructed through local networks in these regions. If we randomly sample cells from a local network in which the selective responses to complex features are constructed by integrating simple features, the sample should include cells with various levels of selectivity. Cells located close to the input end should be maximally activated by simple features, cells close to the output end should respond only to the complex features, and cells at intermediate stages should show some intermediate properties. The areas that satisfy this condition were TEO and V4. It may be proposed that the selectivity to features of medium complexity is mainly constructed in local networks in TEO and V4.

Although we did not find clear evidence of selectivity to complex features in V2, slightly stronger responses to a complex pattern than the best simple stimulus (bar or grating) may not be unusual among cells in V1 (Lehky et al 1992). Selectivity to moderately complex features may gradually develop throughout the lower stages and become apparent in V4 and TEO.

The anatomical organization of the forward projection from TEO to TE is consistent with the idea that the selectivity to moderately complex features is already developed in the circuit up to TEO. We injected an anterograde tracer, PHA-L, into a single small region (the horizontal width of the injection sites

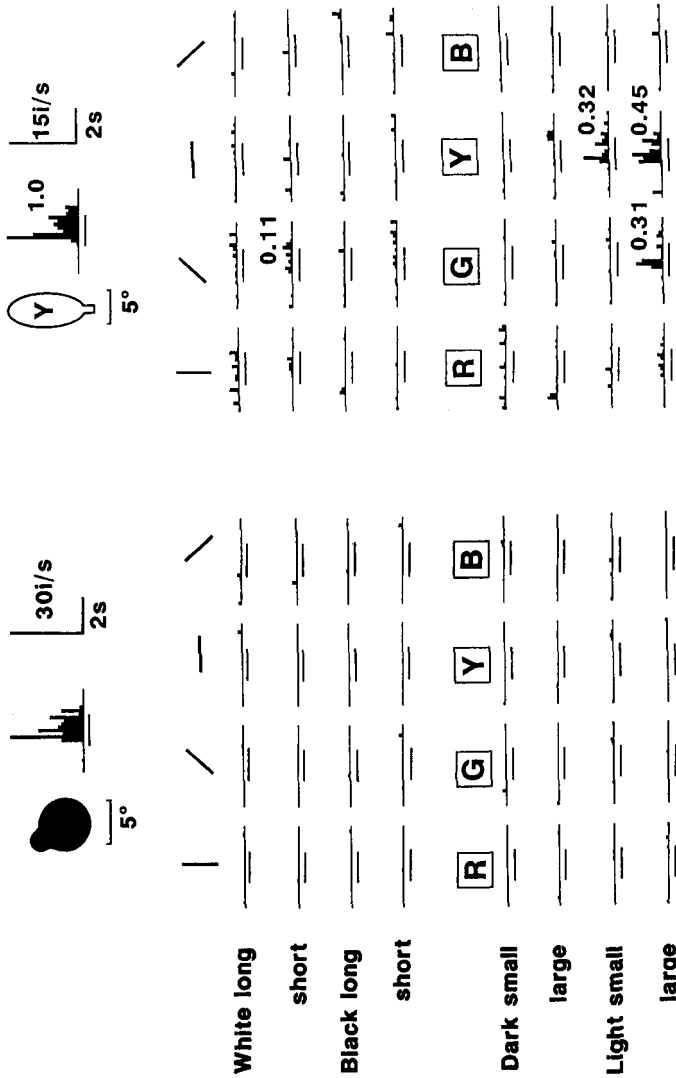


Figure 9 Responses of a TE cell (*left*) and TEO cell (*right*) to a set of simple stimuli. Their responses to individually determined critical features are shown at the top.

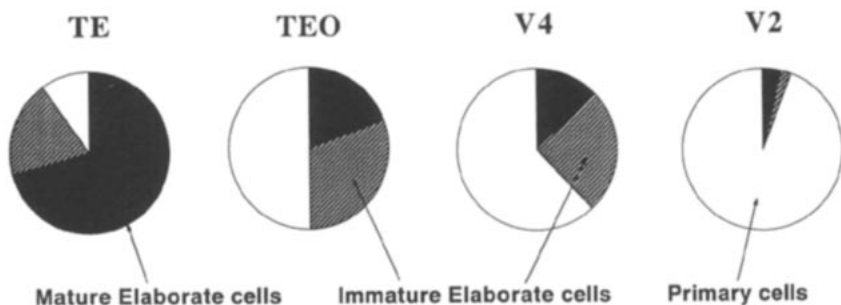


Figure 10 Proportion of cells with different levels of selectivity to complex features. The maximum response to the simple stimuli was <0.25 of the response to the complex critical feature for mature elaborate cells, between 0.25 and 0.75 for immature elaborate cells, and >0.75 for primary cells.

was 330 to $600 \mu\text{m}$) of the part of TEO representing the central visual field, and observed labeled axon terminals in TE (Saleem et al 1993b). Labeled terminals were nearly limited to three to five focal regions in TE (Figure 11). In each of the projection foci, the labeled terminals were not limited to the middle layers, but were distributed to form a columnar region encompassing from layer 1 to 6. The horizontal width of the columnar foci was 200 to $380 \mu\text{m}$, which was slightly smaller than the physiologically determined width of columns in TE. As noted above, the receptive fields of cells in TE are large and usually include the fovea; no retinotopical organization has been found in TE. Thus, the specificity of the TEO to TE connections should be defined in the feature space but not in the retinotopical space. Outputs from a single site of TEO may carry information about a particular complex feature, and they are sent, therefore, only to a limited number of foci in TE.

Although the overall distribution of labeled terminals was elongated to form a columnar region, this does not necessarily mean that individual axons make arbors in columnar regions. Indeed, single axons reconstructed from serial sections were heterogeneous in shape. Some axons terminated exclusively in layer 4 and the bottom of layer 3. Some other axons terminated only in layers 1 and 2. Single axons also terminated in elongated regions, including both the middle and superficial layers. A single site in TEO may send many different kinds of information about a complex feature to a column in TE, and the different kinds of information interact with each other through the local network within the TE column.

Thus, there are two things first achieved in TE: One is the columnar organization, namely, arrangement of cells with overlapping and slightly different selectivity in local columnar regions; and the other is the invariance of responses for the stimulus position. The receptive fields of cells in TE are large

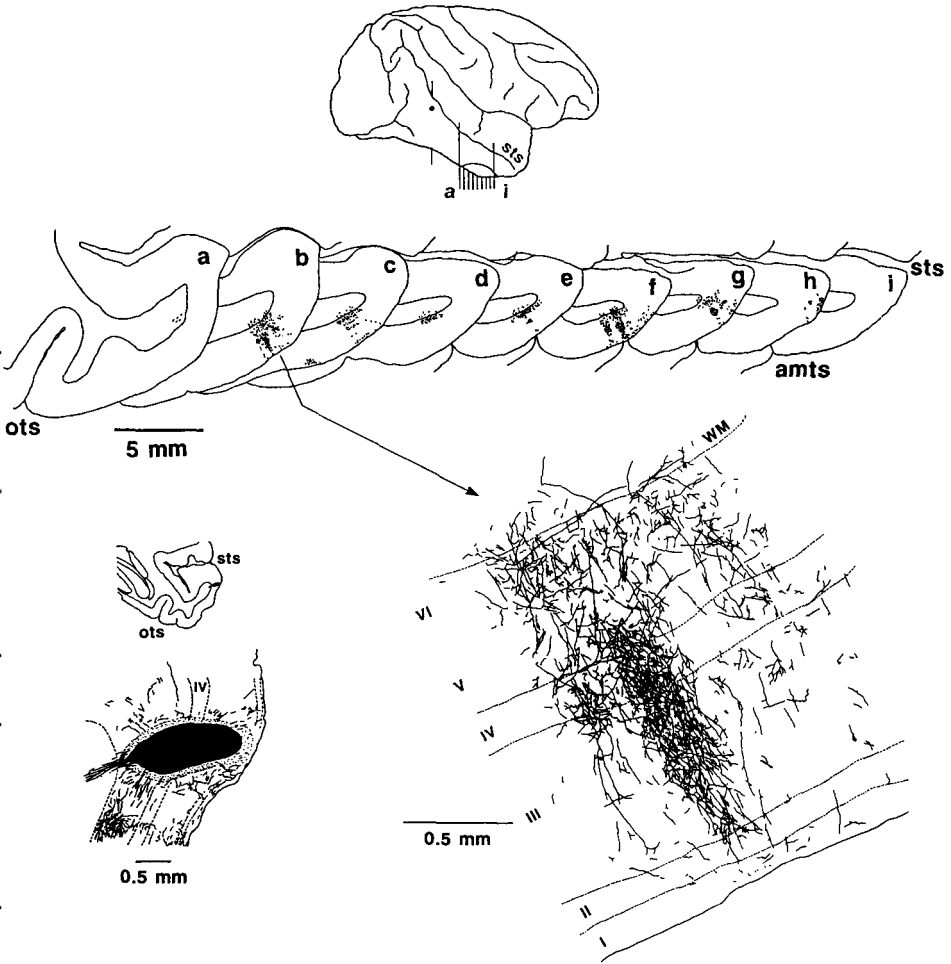


Figure 11 Distribution of labeled axon terminals in TE after a single focal injection of PHA-L into TEO.

and include the fovea, and the selectivity of responses is essentially constant throughout the large receptive fields. A significant part of cells in TEO and V4 respond to moderately complex stimuli, as in TE. However, the receptive fields of the cells in TEO and V4 are still much smaller than those of cells in TE and are retinotopically organized (Boussaoud et al 1991, Kobatake & Tanaka 1994). This means that there are two steps in the formation of cells responding to integrated features with invariance to changes in stimulus posi-

tion. First, the selectivity is constructed for stimuli at a particular retinal position in TEO and V4; then, the invariance is achieved in TE by obtaining inputs of the same selectivity but with the receptive fields at different retinal positions.

One problem with this two-step structure is that individual cells or columns in TE each require a set of input cells with receptive fields distributed over the large receptive fields of the TE cells. Because the central visual field is magnified in TEO (Boussaoud et al 1991, Kobatake & Tanaka 1994), cells in the peripheral TEO may not be sufficiently numerous to extract the great number of integrated features. I would raise the possibility that the inputs from the peripheral TEO convey information on primitive features and that the selectivity in the periphery is constructed at synapses of TE cells. The selectivity can be generalized in TE cells from the central to the peripheral visual field by modifying the synapses of the peripheral inputs according to the generalized Hebbian rule (Földiák 1991) whenever the object containing the critical feature moves from the center to the periphery in the visual field. The selective inputs from the central TEO are used as seeds. This hypothesis can be tested by examining properties of responses of cells in the part of TEO representing the peripheral visual field.

Optical Imaging of the Columnar Organization

To further study the spatial properties of columnar organization in TE, we have introduced the technique of optical imaging (Wang et al 1994). The intrinsic signals, which are thought to originate in the increase of deoxidized hemoglobin in capillaries around elevated neuronal activities (Frostig et al 1990), were measured. The cortical surface was exposed and illuminated with red light tuned to 605 nm with 10-nm bandwidth. Activated neuronal tissue takes oxygen from hemoglobin, so the density of deoxidized hemoglobin in nearby capillaries increases. Because deoxidized hemoglobin absorbs much more light than oxidized hemoglobin at that wavelength, the region of cortex with elevated neuronal activities becomes darker in the reflected image.

To find visual stimuli that would be effective for the part of TE later exposed for optical imaging and to establish the relation between the optical changes and elevated neuronal activities in TE, we combined electrophysiological recordings from single cells with the optical imaging. The single-cell recordings were conducted in separate sessions prior to the optical imaging session. The critical features were determined for 15 to 25 cells recorded in 6 to 8 penetrations at different sites. The optical imaging was performed with the critical features and some other control stimuli. Five to 25 different stimuli were used and each of them was presented 24 or 40 times each for 4 s. The raw images for individual stimuli were divided by the image obtained while

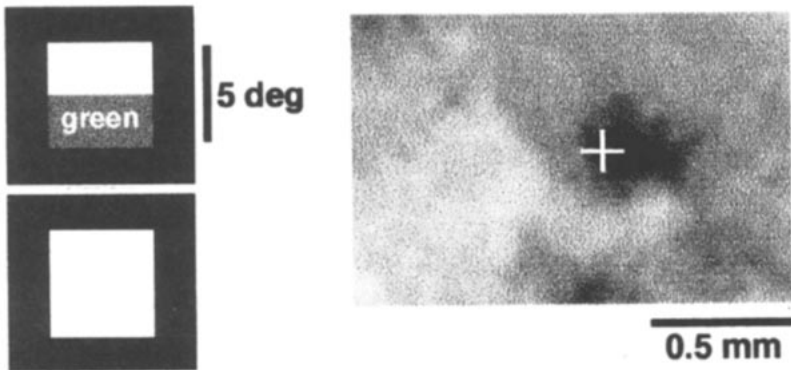


Figure 12 Optical imaging of a column responding to a combination of a green rectangle and white one. The image was obtained by dividing the image obtained while the monkey saw the stimulus by the image during stimulation with a white square. The cross mark indicates the site of the electrode penetration at which the stimulus was determined as the critical feature of one cell.

the monkey saw a blank screen without stimuli to remove the basic level unrelated with the visual stimuli, and the images for the critical features were divided by those for their null component stimuli that were not effective for the activation of cells to remove the activation due to the component features.

Each of the critical features determined in the preceding unit-recording sessions activated one to seven dark spots within the imaged region of TE (3.3 mm by 6.1 mm). The locations of the spots were different for different features, and one of the spots covered the site of the electrode penetration from which the critical feature was determined (Figure 12). The average diameter of individual spots was 490 μm , which roughly coincided with the width of columns in TE inferred by the unit-recording experiments (Fujita et al 1991). The features should have activated a large proportion of cells within the region to evoke the observable metabolic change. Thus, clustering of cells that responded to a moderately complex feature was confirmed.

The set of visual stimuli used in one block of optical imaging included three critical features, which were determined for three different cells recorded in the same penetration. Two of them were combinations of two regions with different luminosity of the same or similar color, and the third one included a gradation of luminosity (Figure 13). The three stimuli all evoked dark spots around the site of the electrode penetration. All of the spots covered the site of the penetration, but they extended to different directions from the site (Figure 13). Each of the spots was about 500 μm in size, and the size of the overall region was 1100 μm . The three stimuli are similar to each other in that they commonly contain a change in luminosity.

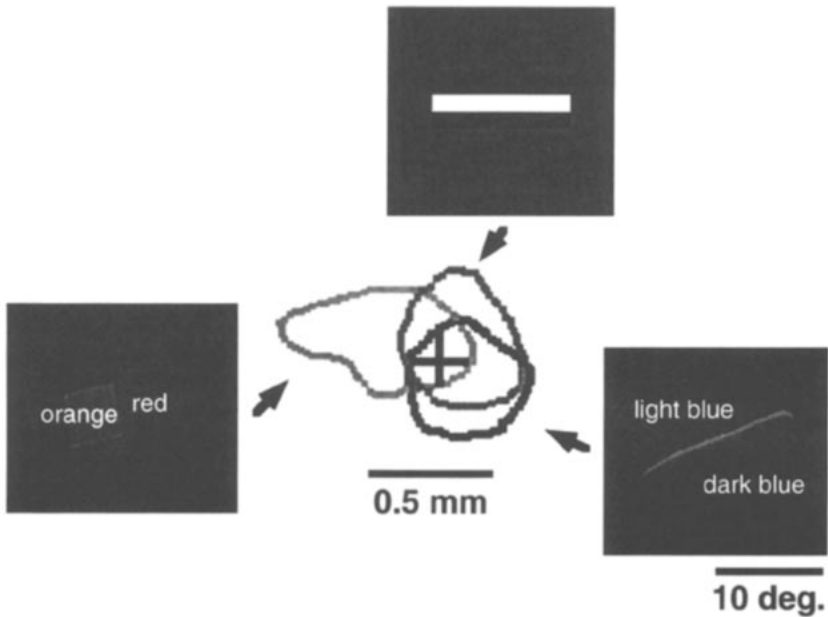


Figure 13 Overlap of activation spots evoked by three critical features determined for three different cells recorded in the same penetration. Only the outlines of the spots at $1/e$ drop from the peak are shown. The cross mark indicates the site of the electrode penetration.

Partially overlapped activation by similar stimuli was also observed with a series of faces of different viewing angles. All of the five cells recorded in an electrode penetration selectively responded to the sight of a face. The image of a face could be simplified to a combination of the eyes and nose for one of them, but we failed to find simpler stimuli for the remaining four cells. Three of the five maximally responded to front faces, and the other two maximally responded to profiles. In the optical imaging experiment, all of the face stimuli evoked activation spots around the penetration (we failed to recover the exact location of the electrode penetration in this case), and the center position of the spots systematically moved in one direction as the face turned from the left profile to the right profile through the front and 45° faces. Individual spots were 300 to 400 μm in size and the overall region covered by them was 800 μm in the long axis along which the center of spots moved.

These facts may suggest that several columns that represent different but related features overlap with one another and as a whole compose a larger-scale unit in TED. The face case further suggests that the arrangement of features within the larger-scale unit has some rule, that is, some space of complex

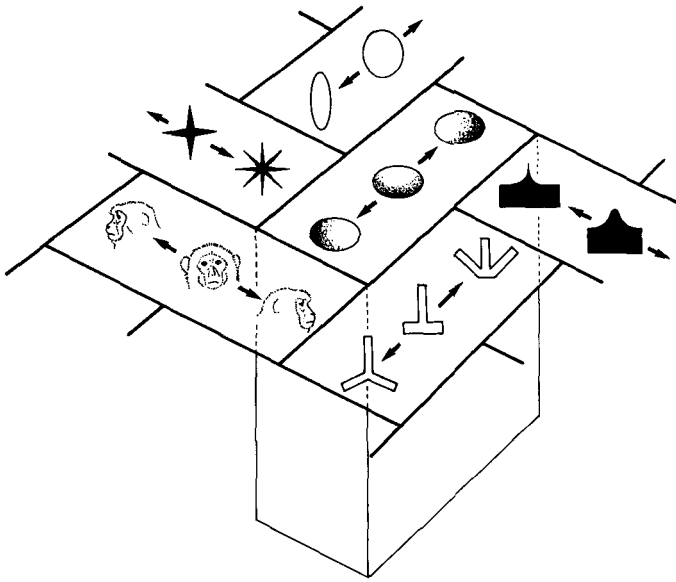


Figure 14 Revised scheme of columnar organization in TE.

features is continuously mapped (Figure 14). Whether the mapping is continuous throughout a large part of TE_d or discontinuous between the units that are probably around 1 mm in size is still unknown. Considering that the dimension of the feature space that TE_d should represent is so high, the latter is more likely.

Changeability of the Selectivity in the Adult

The selectivity to complex critical features can change as a result of changes in the visual environment in the adult. We have trained two adult monkeys to discriminate 28 moderately complex shapes with a stand-alone apparatus—including a display, a computer, and a touch screen—by using a task similar to the delayed-matching-to-sample (Kobatake et al 1992, 1993). One stimulus, randomly selected from the 28 stimuli, appeared on the display (sample stimulus) and disappeared by the monkey's touching it. After a 16-s delay with a blank screen, 5 shapes, including the sample, appeared on the display. The monkey had to select the sample and touch it to get a drop of juice. After a year of training, the monkeys were prepared for repeated recordings. The recordings were performed from cells in TE_d under anesthesia. We determined for individual cells the best stimulus from the set of animal and plant models

that we had previously prepared to investigate the critical features in naive monkeys. The response to the best object stimulus was then compared with responses of the same cell to the shape stimuli used in the training. We did not perform the reduction process in this experiment for the sake of time.

In TE of the trained monkeys, about 25% of cells gave a maximum response to some of the stimuli used in the training. Conversely, 5% of TE cells in untrained animals responded maximally to these stimuli. These results indicate that the number of cells that responded to training stimuli increased owing to the 1-year-long discrimination training. However, the spatial organization of the modified cells in the cortex has yet to be studied. We do not know whether new columns were formed for the discrimination of training stimuli or whether cells distributed over many columns present since before the training were tuned to the training stimuli. Whether or not similar changes happened in TEO and V4, and the time course of the change also are still unknown.

Sakai & Miyashita (1991) have shown effects of discriminatory training in the adult on the stimulus selectivity of TE cells, although indirectly. The task paradigm they used in the training was associative pair matching. The stimuli were composites of Fourier descriptors. They arbitrarily made 12 pairs of stimuli, and the monkeys were asked to select the member of the pair in response to the other member of the pair. One of the stimuli appeared as the sample, and after a delay period, two stimuli, including the stimulus paired to the sample, appeared. The monkey had to touch the paired stimulus to get a reward. After training for about a month, through which the association was learned, recording of TE cells was started by using the same task paradigm. Some cells responded to the two stimuli composing the pairs, and the pairing was shown to be significantly more frequent than that expected by chance. Considering that the pairs of stimuli were made arbitrarily from infinite possibilities, the dual responsiveness of the cells to the paired stimuli should have been formed through the adult learning.

There are two studies that show that responses of cells in TE and surrounding regions change within the course of recording from the same single cell. Miller and colleagues (Miller & Desimone 1991, Li et al 1993) found that as the newly introduced stimulus became familiar, responses of cells at the border region between TE and the perirhinal cortex to the stimuli gradually decreased. This effect is discriminated from the habituation of responses to successive presentation of the same stimulus, because the decrease occurred even after several intervening presentations of different stimuli. However, because the changes that Miller and colleagues observed were opposite to those we observed after the long training, the two phenomena are not likely to be related. Rolls et al (1989) found that responses of cells in TE and the ventral bank of the superior temporal sulcus to faces changed rather rapidly after an introduction of a new set of faces. The changes of the responses to faces included both an increase and a decrease of the

responses. Because the immediate changes that Rolls et al observed were relative changes among responses to similar stimuli (faces), they may be different from the changes of stimulus selectivity after long-lasting training, which should be changes among more different stimuli.

Functions of the TE Columns

The columnar organization suggests that an object feature is not represented by activity of a single cell but by the activity of many cells within a single columnar module. Representation by multiple cells in a columnar module, in which the selectivity varied from cell to cell while effective stimuli largely overlapped, can satisfy two apparently conflicting requirements in visual recognition: robustness to subtle changes in input images and preciseness of representation. Whereas the image of an object projected to the retina changes owing to changes in illumination, viewing angle, and articulation of the object, the global organization of outputs from TE should be little changes. The clustering of cells with overlapping and slightly different selectivity works as a buffer to absorb the changes.

The representation by multiple cells with overlapping selectivity can be more precise than a mere summation of representation by individual cells. A similar argument has been made for hyperacuity (Erickson 1968, Snippe & Koenderink 1992). The position of the receptive fields changes gradually in the retina, with a large overlap among nearby cells. By taking the difference between the activity of nearby cells, an acuity much smaller than the size of the receptive fields is produced. A similar mechanism to that in retinal space may work in feature space with largely overlapping and gradually changing selectivity, as suggested by Edelman (1995). A subtle change in a particular feature, which does not markedly change the activity of individual cells, can be coded by the differences in the activity of cells with overlapping and slightly different selectivity.

The function of the columnar organization in TE_d may go beyond the discrimination of input images. The optical imaging experiments suggested that there is a continuous mapping of features within cortical units about 1 mm in size across the cortical surface. There may be a twofold functional significance to this continuous mapping. First, an evenly distributed variety of cell properties is made along the feature axis. The continuous mapping may be a tool to make the full divergence without omission (Malach 1994, Purves et al 1992). Second, computations are conducted involving the varied features based on the local neuronal connections between the cells representing the varied features. The computations may be to transfer the image of an object for 3D rotations or production of the image at different illumination conditions or at different articulation poses.

A series of studies recently performed in slices of the rat motor cortex suggest that there are two kinds of connections between pyramidal neurons through their axon collaterals (Thomson & Deuchars 1994). Pyramidal cells located within a narrow columnar region 50 to 100 μm in width are tightly connected by synapses on the basal dendrites or the proximal part of the apical dendrites. They tend to fire together by sharp-rising big excitatory postsynaptic potentials (EPSPs) exerted through these connections. Another anatomical structure gives similar response properties to pyramidal cells within a narrow column. The shafts of their apical dendrites get close to compose a bundle, on which input axons may make synapses without discrimination (Peters & Yilmaz 1993). This narrow column corresponds to the "minicolumn" of Mountcastle (1978). In contrast, pyramidal cells with a longer horizontal distance are connected by synapses at the distal part of the apical dendrites. The EPSPs are small and slowly rising, although they are long-lasting: They may contain NMDA-type glutamate receptors.

Taken together, we may draw a schema of area TE that cells within the minicolumn compose a unit by receiving common inputs and exciting each other and that nearby minicolumns exert long-lasting but weak excitatory inputs to each other. After a minicolumn is activated by the retinal visual input, subthreshold activation propagates from it to nearby minicolumns, forming a pattern of activation with a focus. The focus of activation may move from one minicolumn to another, through interaction with distant activation foci in TE or interaction with the other brain sites (as will be described in the section on object recognition by activities distributed over the brain). This mechanism may be used for various kinds of computation that the visual system has to conduct to realize the flexibility of visual recognition, such as transfer of the image of an object for 3D rotations, production of the image at different illumination conditions, and in the case of faces, production of the image with different expressions. Thus, the columnar organization of TE may provide an overlapping and continuous representation of object features, upon which various kinds of calculations can be performed.

Binding Activities in Distant Columns

Because object features to which individual TE cells respond are only moderately complex and because cells within a single column respond to similar features, the calculation performed within a column can provide only information on partial (but not necessarily local) features of object images. To represent the whole image of an object, calculation in several different columns must be combined. This evokes the problem of *binding*, that is, how to discriminate different sets of activity when there are more than two objects in the nearby retinal positions. The receptive fields of TE cells are too large to

discriminate different objects according to their retinal positions. I examine in a later section whether there are single cells anywhere in the brain that represent the concept of objects through their activity alone. The problem of binding exists regardless of the presence or absence of such concept units in brain sites beyond TE. The concept units, if present, have to discriminate different sets of TE activity originating in different objects.

One possible mechanism to solve the problem is the synchronization of firings (Engel et al 1992, Singer 1993). If firing of cells that originates from the image of the same object is synchronized and if firing that originates from different objects is desynchronized, the different sets of firings will be discriminated from each other. Firing synchronized with oscillations has been found between cells in the cat visual cortex, and some context dependency of the synchronization has also been reported. Although oscillating firing has not been found in TE (Young et al 1992, Tovee & Rolls 1992), nonperiodic synchronization may be present in TE.

Another possible mechanism of binding in TE is selection by attention (Crick 1984). We can pay attention to only one, or a few at most, object at a time. If the representation of features of an attended object is enhanced and that of other objects is suppressed, the binding problem will disappear. This mechanism is likely to be working, because strong effects of attention have been found on responses of TE cells (Richmond & Sato 1987, Moran & Desimone 1985, Spitzer et al 1988, Chelazi et al 1993).

A third possibility is that the set of distant activity in TE originating from a single object is combined by making loops of activity with activity in retinotopically organized former stages in the ventral pathway. TE projects back to TEO, V4, V2, and even V1 (Rockland et al 1994, Rockland & Van Hoesen 1994). There are also step-by-step feedback projections. Different sets of activity originating from different objects are discriminated by the position of combined activity on the retinotopical maps. Kawato et al (1991, 1993) have indicated the importance of feedback projections from a similar viewpoint.

Responses to Complex Object Features in Other Brain Sites

Is there any brain site that contains cells selectively responding to more integrated features than the critical features determined in TED? One group of candidates are the brain sites to which TED projects: the polysensory area in the anterior part of the superior temporal sulcus (STPa), the prefrontal cortex, the perirhinal cortex, the amygdala, and the striatum of the basal ganglia. Visually responsive cells have been reported in all of these sites.

Cells that selectively responded to the sight of a face were found in STPa in the early 1980s (Bruce et al 1981; Yamane et al 1988; Perrett et al 1982,

1987; Young & Yamane 1992; Rolls 1992), and such cells, which were so-called face neurons, have been extensively studied. There are reports that such cells are also present in TE itself (Baylis et al 1987, Tanaka et al 1991), area TG (Nakamura et al 1994), and the amygdala (Leonard et al 1985, Nakamura et al 1992). The meaning of selective varied among these studies: In some of the studies only several non-face stimuli were presented, and most of the studies did not test partial features of the image of a face. However, a few of them used a scrambled face, which was made with scrambled patches of the picture of a face, and showed that the scrambled face was not effective (Bruce et al 1981). A few studies found that there were cells that were not activated by a face without the eye or by the eye only (Perrett et al 1982, Rolls et al 1985). We found systematically arranged columns in TED that respond to different views of faces. These data suggest that there are cells that require all the essential features that compose the image of a face. The image of a face is more complex than the other features represented by cells in TED.

The presence of face neurons cannot be generalized to the representation of other objects. Faces of monkeys are special for monkeys, and also those of human beings for laboratory monkeys, in that faces are important media for social communication between individuals. Discrimination of faces from other objects is only a preliminary stage to represent information of expressions or features of individual faces. This view is supported by the fact that there are cells that respond to the view of body movements or hand actions in STPa (Perrett et al 1985, 1989, 1992; Oram & Perrett 1994). Body movements and hand actions often express important information about the relation between individuals in the scene or between the individual in the scene and the observer. These groups of cells in STPa may be specially prepared for social communication.

Responses specific to the color or shape of visual stimuli have been found in the principal region and inferior convexity of the prefrontal cortex (Fuster et al 1982, Watanabe 1986, Wilson et al 1993). Watanabe (1986) found specific responses by using green and red squares, or a disk and perpendicular grating. Wilson et al (1993) examined cells in the inferior convexity with a larger variety of stimuli, including faces. Some of the cells that Wilson et al studied specifically responded to a face, although the feature critical for the activation was not identified in this study. Interestingly, responses of many of the cells that Watanabe studied were not determined by the attributes of the stimuli but by the temporal meaning of the stimulus attributes in the behavioral frameworks. Watanabe demonstrated this by changing the behavioral meaning of the same stimuli by the cue signal presented prior to the stimuli. The main computation conducted in the prefrontal cortex on the images of visual stimuli may be to relate the inputs to the temporal behavioral frameworks.

Visual responses with various level of stimulus selectivity have been found

in the amygdala (Ono et al 1983, Nishijo et al 1988, Nakamura et al 1992). Many cells responded selectively to a category of objects that might cause a certain kind of emotion. This view is consistent with a general idea that the amygdala is essential for emotion (Turner et al 1980). A main function of the amygdala, from the viewpoint of visual object recognition, seems to be the association of sensory inputs to different kinds of emotion. A question is whether the association takes place after inputs representing a particular object are denoted by activity of a single group of cells. Nishijo et al (1988) and Nakamura et al (1992) reported that some cells in the amygdala responded selectively to particular objects. However, because the variety of reference stimuli used in these studies was not very extensive, the tuning property of the cells may not be sharp enough, and a kind of population coding such as that in TED is directly associated with different kinds of emotion.

Miller & Desimone (1991) and Nakamura et al (1994) have conducted recordings from the perirhinal cortex. Miller & Desimone used six arbitrarily chosen pictures of natural objects and found that most of them activated the cells, although their effectiveness was different. These facts may suggest that selectivity of cells in the perirhinal cortex is more gradual than that of cells in TED. Nakamura et al examined cells in TE as well as the perirhinal cortex and the TG part of it (polar cortex) with a larger variety of stimuli and concluded that cells in the perirhinal cortex and TG were as selective as those in TE.

The data of our anatomical studies, in which an anterograde tracer, PHA-L, was injected into a single site in TED and the ventral part of TE (TEv), indicated that the projection from TE to the perirhinal cortex diverges: A single site in TE projects to a large part of area 36 of the perirhinal cortex (Saleem et al 1993a, 1994). Because this divergent projection was found regardless of the injection site in TE, a single site in the perirhinal cortex should receive convergent inputs from multiple sites in TE. This anatomical structure provides the opportunity for interaction between different features represented by distant columns in TE. Information processing in the perirhinal cortex may be more associative than discriminative.

The recent finding by Miyashita et al (1994) is consistent with this idea. They trained monkeys for the association of two different pictures (see section on changeability of the selectivity in the adult). The commissural connections of the monkey had been destroyed. After the association of several pairs was learned, the perirhinal cortex and the entorhinal cortex that connects the perirhinal cortex to the hippocampus were destroyed by injecting ibotenic acid. There were TE cells that responded to two paired stimuli before the lesion, but such cells disappeared after the lesion. This disappearance indicates that the dual responsiveness to two paired stimuli was underlined by a network that included the perirhinal cortex. The associative aspect of information processing in the perirhinal cortex may also underlie its importance for performing the delayed-

matching-to-sample (DMS) with visual images of objects (Murray & Mishkin 1986, Zola-Morgan et al 1989, Meunier et al 1993, Eacott et al 1994).

Finally, we need to discuss TEv. The part of TE medial to the anterior middle temporal sulcus (AMTS) has been referred to as TEv. Martin-Elkins & Horel (1992) and Yuki et al (1992) found that afferent pathways to TE_d and TEv are separate: TE_d receives inputs via the lateral part of the posterior IT, whereas TEv received inputs from regions at the ventral surface. Iwai & Yuki (1987) found that TE_d and TEv have different projection patterns to the amygdala. We have also recently found that TE_d and TEv have different projection patterns to the perirhinal cortex, prefrontal cortex, and striatum, as well as to the amygdala (Cheng et al 1993, Saleem et al 1994). TE_d and TEv thus seem to represent inferotemporal stages of parallel pathways. Because projections to the perirhinal cortex, which is thought to be important for visual DMS, are more numerous from TEv than from TE_d (Saleem et al 1994), it is hypothesized that TEv is more involved in visual memory than TE_d. The stimulus selectivity of cells in TEv may be different from that of cells in TE_d, although there have been no studies that explicitly conducted the comparison.

In summary, there have been no firm findings of cells that responded only to features more integrated than the critical features found for TE_d cells, except for the cells in STP_a responding to faces. The cells in STP_a are thought to be specially prepared to convey information for social communication among monkeys. There is some evidence suggesting that cells in the prefrontal cortex are organized to relate visual stimuli to temporal behavioral frames and that those in the amygdala are organized to relate visual stimuli to specific emotion of the monkey.

Object Recognition by Activities Distributed over the Brain

Sakata and his colleagues have recently found shape-selective cell activities in the parietal areas in the intraparietal sulcus (Taira et al 1990, Sakata & Kusunoki 1992). Many cells in the lateral bank of the sulcus selectively responded to visual images of switches that the monkey was trained to manipulate. The monkey reached the switches and pulled them. The switches varied in shape, so the monkey shaped its hand differently before it reached for different switches. Because the discharges started when the monkey saw the switches and because the discharges decreased when the task was performed in a dark room, the discharges should be caused, at least partially, by the visual inputs.

Sakata and colleagues further found that some cells in the more posterior part of the sulcus responded to more primitive features of stimuli, including the 3D orientation of a pole and the 3D tilt of a plane. They presented the stimuli on a computer graphic system with binocular disparity (Kusunoki et al 1993; Tanaka et al 1992, 1994). The responses were reduced when the binocular disparity was

removed, which indicates that the binocular disparity gave an essential cue for the responses.

Taken together, there seems to be a flow of information of 3D shapes of objects that the monkey may manipulate. These findings coincide with the proposition by Goodale and colleagues (1991, 1992), based on human clinical data, that the dorsal pathway leading to the parietal cortex is responsible for visuo-motor control, but not for spatial vision (Mishkin et al 1983). To manipulate an object, the object's 3D structure should be perceived. There may be an independent representation of the shape of objects in the dorsal pathway that is independent of the representation of objects in the ventral pathway; and probably only course shape is represented. This dorsal representation of objects may influence the representation of objects in the ventral pathway through the indirect connection via the parahippocampal structures (Van Hoesen 1982, Suzuki & Amaral 1995) or via regions in the superior temporal sulcus (Seltzer & Pandya 1978, 1984, 1989, 1994).

The accumulated findings favor the idea that no cognition units represent the concept of objects; instead the concept of objects is found only in the activities distributed over various regions in the brain. When the visual image of an object is given, it is processed in the ventral visual pathway, and the representation containing similarity to other objects and association with images of the same object under different conditions is reconstructed there. This representation in the ventral visual pathway utilizes the population coding in two levels. First, the image of the object is represented by a combination of multiple partial (but not necessarily local) features designated by different columns in TE. Because the presence of the partial features is represented in an analog manner, the combinatorial representation can be understood as a combination of similarity to different prototypes of object images (Edelman 1995). The second level of population coding is in the representation of partial features. The features are represented by multiple cells within a TE column that has overlapping selectivity. This level of population coding has been extensively discussed in the section on functions of the TE columns. Triggered by inputs from the IT, emotional information of the object is read out in the amygdala; association with other objects is read out through the perirhinal cortex; and behavioral significance emerges in the prefrontal cortex. The visual image of the object is also processed in the dorsal pathway, and information necessary for the monkey to manipulate the object is read out in the parietal cortex. All this recovered information of the object, distributed over the brain, may represent the concept of the object.

Conclusions

Cells in area TE of the IT selectively respond to various moderately complex object features, and those that respond to similar features cluster in a columnar

region elongated perpendicular to the cortical surface. Although cells within a column respond to similar features, their selectivity is not necessarily identical. The data of optical imaging in TE have suggested that the borders between neighboring columns are not discrete; there is a continuous mapping of complex feature space within a larger region containing several partially overlapped columns. This continuous mapping may be used for various computations, such as production of the image of the object at different viewing angles, illumination conditions, and articulation poses.

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