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Neuronal Mechanisms of Object Recognition

Keiji Tanaka

Recognition of objects from 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 like the vision in lower animals but is a flexible process in which considerable change in images, resulting from different illumination, viewing angle, and articulation of the object, can be tolerated. Recent experimental findings about the representation of object images in the inferotemporal cortex, a brain structure that is thought to be essential for object vision, are summarized and discussed in relation to the computational frames proposed for object recognition.

Almost 30 visual areas have been identified in the cerebral cortex of the macaque monkey, and many of them can be organized into two anatomical pathways: the ventral pathway directed toward the inferotemporal cortex (IT) and the dorsal pathway directed toward the inferior parietal lobule. The two pathways are also functionally distinguishing: The ventral pathway is thought to be responsible for object vision, and the dorsal pathway for space vision or visuomotor control (*1*). The ventral pathway runs from cortical area V1 to V2, thereafter to V4, and finally to the IT. This pathway is thought to be essential for object vision because monkeys that have had their IT bilaterally ablated show severe and selective deficits in learning tasks that require the visual recognition of objects (*2*). The IT is further divided into the posterior IT, or TEO, and the anterior IT, or TE. The projection from V4 that terminates in TEO is more dense than that to TE, and TEO projects to the most posterior-anterior extent of TE. The IT projects to various structures 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 the anterior part of TE, than from the areas at earlier stages. Therefore, there is a sequential cortical pathway from V1 to TE, and outputs from the pathway originate mainly in TE.

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Columnar Organization in TE

An obstacle in the study of neuronal mechanisms of object vision has made the determination of the stimulus selectivity of individual cells difficult: There is a great variety of object features in the natural world, and if perception is based on a calculation that is nonlinear (which is very plausible), the variety cannot be represented by an arbitrary set of "basic" features. We developed a systematic reduction method in which the study of selectivity was started with many natural objects, and the complexity of the effective stimuli was reduced to determine the features critical for activation of individual cells (*3, 4*). Some previous studies

used a similar method (5). The procedure involves two steps: First, we presented many three-dimensional animal and plant representations to find the effective stimuli; second, we simplified the images of the effective stimuli by sequentially removing a part of the features contained in the image to determine the necessary and sufficient characteristics for the maximal activation of the cell. The latter step was first performed with paper cutouts (3), but a computer system has now been developed (4). Images of the effective objects are taken with a video camera and then simplified, and pictures are drawn to simulate a part of the features contained in the image. Figure 1 exemplifies the process for a cell for which the effective stimulus was reduced from a dorsal view of the head of an imitation tiger to a combination of a pair of black rectangles and a white square.

Using this procedure, we found that most cells in TE required moderately complex features for their activation (Fig. 2) (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 shapes that were moderately complex, whereas others were combinations of such shapes with color or texture. The individual critical features were not complex enough to specify a particular object seen in nature through activation of a single cell. Activation of a few to several tens of cells with different critical features seems necessary to specify a particular natural object.

By recording from more than two cells simultaneously with a single electrode, we found that cells located at nearby positions in the cortex have a similar stimulus selectivity (4). The critical feature of one isolated cell was determined by the procedure described above, and 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.

We then made vertical and oblique penetrations through TE (4). The critical feature of a cell located at the middle of the penetration was first determined. A set of stimuli, including the optimal, suboptimal, and ineffective stimuli for the first tested cell, was made and then used to test the responsiveness of other cells recorded at different positions along the same penetration. Cells that responded to related stimuli in the stimulus set, that is, stimuli that were identical or similar to the optimal stimulus for the first cell, covered most areas of the vertical penetrations, but were limited to a span of several hundred micrometers in the oblique penetrations (average, 400 μm).

The TE region is thus composed of columnar modules, like those in V1, in which cells with overlapping but slightly different selectivity cluster together (Fig. 3). The width of a columnar module across the cortical surface may be slightly greater than 400 μm; 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 TE into 500 μm by 500 μm squares, is 1300. This columnar organization may be crucial to the representation of object images in TE.

Functions of the TE Columns

The columnar organization suggests that an object feature is not represented by the 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 varies from cell to cell and effective stimuli largely overlap can satisfy two apparently conflicting requirements in visual recognition: robustness to subtle changes in input images and precision of representation. Whereas the image of an object projected to the retina changes in response to variations in illumination, viewing angle, and articulation of the object, the global organization of outputs from TE changes little. The clustering of cells with overlapping and slightly different selectivity works as a buffer to absorb the changes. General advantages of the distributed representation have been extensively discussed elsewhere (6).

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 (7). The position of the receptive fields changes gradually in the retina with a large overlap

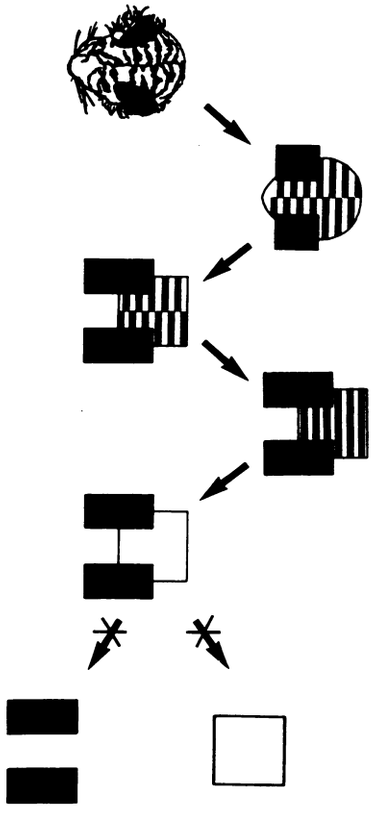

Fig. 1. An example of the procedure to determine the critical feature for activation of single cells: the gradual reduction of the complexity of the image of effective object stimuli. The substitution of intermediate features for the image of a tiger head, down to a combination of a white square with a pair of black rectangles, did not reduce the magnitude of the response. Further decomposition eliminated the response.

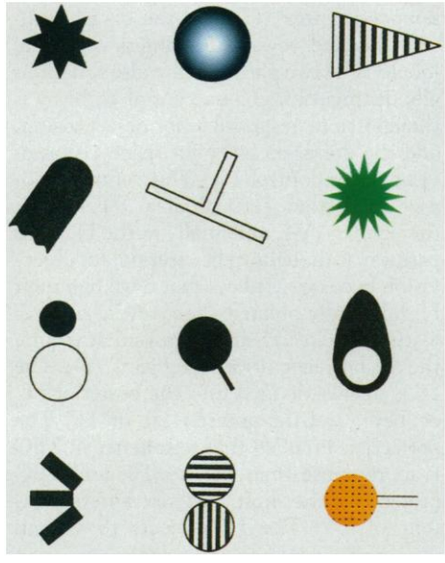

Fig. 2. Twelve examples of the critical features for the activation of single cells in area TE.

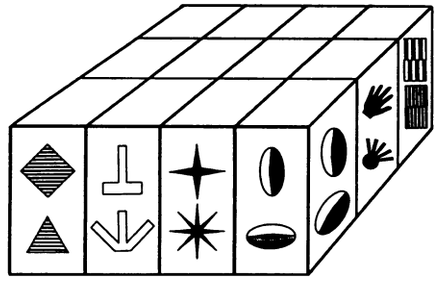

Fig. 3. Schematic diagram of the columnar organization in TE. Cells with similar but slightly different selectivity cluster in elongated vertical columns, perpendicular to the cortical surface.

among nearby cells. With the use of the difference between the activity of nearby cells, an acuity much smaller than the size of the receptive fields is produced. A mechanism similar to that in retinal space may work in feature space with largely overlapping and gradually changing selectivity, as suggested by Edelman (8). 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 variety of selectivity within single columns may have more functional meanings. In the vertical penetrations made in TE, the selectivity of cells at distant locations tended to differ more than those of cells at closer distances (4). This, however, does not mean that the selectivity changed depending on the layer in which the cell was located. The penetrations could not be exactly aligned with the columns, and the distance between two cells projected to the cortical surface tended to be larger as the distance along the penetration became larger. Therefore, it is possible that the selectivity of cells gradually changes along the axis parallel to the cortical surface within single columns. This means that a variety of object features are systematically represented along the cortical surface in a continuous manner, which is similar to the continuous representation of orientation within the hypercolumns of V1. The width of the columnar modules in TE is closer to the width of the hypercolumns than that of individual orientation columns of V1.

The stimulus selectivity of cells does not change gradually from column to column in TE; rather, there is an apparent discontinuity at the border. This discontinuity may seem inconsistent with the hypothesized principle of continuous representation of object features; however, the discontinuity is inevitable in the representation of integrated features. The object features of moderate complexity compose a feature space of extremely high dimensions, and a space of high dimensions cannot be mapped on a two-dimensional (2D) surface without extensive discontinuities (9).

Thus, the columnar organization of TE may provide an overlapping, and possibly continuous, representation of object features, upon which various kinds of calculations, such as that of similarity between images of different objects (8) and transfer of the image of the same objects for 3D rotations (10), are performed.

Binding Activity in Distant Columns

Because object features to which individual TE cells responded were only moderately complex and cells within a single column responded 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 or several tens of 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.

One possible mechanism to solve the problem is the synchronization of firings (11). If firing of cells that originates in the image of the same object is synchronized and firing that originates in different objects is asynchronous, the different sets of firings can be discriminated. 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 (12). Although oscillating firing has not been found in TE (13), nonperiodic synchronization may be present.

Another possible mechanism of binding in TE is selection by attention (14). We can pay attention to only one 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 disappears. This mechanism is likely because strong effects of attention have been found on responses of TE cells (15).

Invariance to Viewing Angle

Marr (16) claimed that an object image in viewer-centered coordinates should be transformed into an object-centered representation so that the matching of the input can be done with only a single stored representation of the object. He thought it impossible to store all different 2D views of objects in the brain. However, there have been no signs of object-centered representation in TE or earlier stages in the afferent pathway of TE. Responses of cells were almost always selective for the orientation of stimuli.

Accumulating psychophysical evidence suggests that the internal representation of objects is not object-centered in human visual perception (17), and computational analyses have shown that not necessarily all the 2D views have to be stored in the brain. A linear superposition of several 2D views or an interpolation and extrapolation of these views with generalized radial basis functions (10) can construct any 2D view of an object.

In the original explanation of the theoretical analyses, the superposition and the interpolation and extrapolation were performed on the whole images of objects. The operations can also be performed with partial features like those represented in TE if there is a separate mechanism to bind the partial features. The interaction between cells with overlapping but slightly different selectivity in columns of TE can subserve the operations. This possible relation between the recognition of 3D objects and the columnar organization in TE can be systematically studied with use of the preserved plasticity of TE in adult monkeys (see below).

Imagery of Objects

Discharges of IT cells not only reflect the processing of input images but participate in the internal representation of the images of objects. Fuster and Jervey (18) recorded from TE cells of alert, conscious monkeys performing a kind of delayed matching-to-sample task. The task was composed of three phases: presentation of a sample stimulus, delay period with no stimuli, and presentation of a set of stimuli for matching, which included the sample. The monkey had to retain information on the sample stimulus during the delay period. Some TE cells maintained discharges during the delay period, the strength of which depended on the sample stimulus. Color stimuli were used by Fuster and Jervey, but the finding has been generalized to shape stimuli (19). These selective, maintained discharges may constitute the working memory of the sample stimulus. Another candidate for working memory in TE, modulation of responses to stimulus presentation, has been found (20).

Discharges of IT cells may also participate in the representation of imagery. Sakai and Miyashita (21) trained monkeys to remember associations of 12 pairs of different patterns. The task was basically the same as the delayed matching-to-sample. In response to a given sample stimulus, the monkey had to select its pair in the match presentation. Some TE cells selectively responded to one or a few particular patterns when the patterns were presented as sample stimuli. When pattern pairs were presented as the sample, they did not fire upon the sample presentation, whereas their discharge rate gradually increased during the delay period toward the match presentation. These discharges may constitute the monkey's expectation of the stimulus optimal for the cell and representation of imagery.

Formation of the Selectivity

The selective responses to complex features, which were first bound in TE cells, have been traced to earlier stages in the

afferent pathway to TE. We found that cells requiring such complex features for the maximal activation are already present in TEO and V4 (*22*). Gallant and coworkers (*23*) also found that there are cells that respond preferentially to concentric or hyperbolic stripes rather than to straight stripes. The optimal features in these areas include concentric stripes but are much more divergent. Unlike in TE, however, many of the cells in TEO and V4 show moderate responses to some primary features in addition to the maximum response to the complex critical feature, and cells with various levels of selectivity intermingle in single vertical penetrations made in these areas. We take this mixture of various cells as evidence that selectivity is constructed through local networks in these regions. Thus, we propose that the selectivity to features of medium complexity is mainly constructed in local networks in TEO and V4.

The anatomical organization of the forward projection from TEO to TE is consistent with the above idea. A single site in TEO projects to only three to five focal regions in TE, each of which had a size roughly corresponding to the physiologically defined columns (*24*). If outputs from TEO carry information on primary features, outputs from a single site should project to more distributed regions in TE because the information is universal.

There are two things first achieved in TE: columnar organization, namely, the arrangement of cells with overlapping and slightly different selectivity in local regions, and invariance of responses for the stimulus position. The receptive fields of cells in TE are large, including the fovea (*3, 5*), and the selectivity of responses is essentially constant throughout the large receptive fields (*25*). The receptive fields of the cells in TEO and V4 are still much smaller than those of cells in TE and are retinotopically organized (*26, 27*). This means that there are two steps in the formation of cells that respond to integrated features with invariance to changes in stimulus position. First, the selectivity is constructed for stimuli at a particular retinal position in TEO and V4, and then the invariance is achieved in TE as inputs are obtained of the same selectivity but with the receptive fields at different retinal positions. The selection of appropriate inputs can be achieved through a simple self-organizing mechanism, as was proposed by Földiák (*28*) for formation of complex cells in V1. That is, a Hebbian rule generalized over time for the coincidence of pre- and postsynaptic activity automatically gathers inputs representing the same features at different retinal positions as the object changes the position.

A problem in 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 overrepresented in TEO (*26*), cells in the peripheral TEO may not be sufficient in number to extract the great number of integrated features. I suggest that the inputs from the peripheral TEO convey information on primitive features and 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 through the generalized Hebbian rule. The selective inputs from the central TEO are used as seeds.

The selectivity to complex critical features and the columnar organization in TE are not determined by genes or early development in infancy but are subject to changes according to changes in the visual environment in the adult. We trained an adult monkey to discriminate 28 moderately complex shapes (*29*). The training was basically the delayed matching-to-sample and the presentation for matching was composed of five stimuli. After a year of training, recordings from TE were performed in an anesthetized condition. 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 naïve monkeys and compared the response to the best object stimulus with responses of the same cell to the shape stimuli used in the training. In TE of the trained monkey, 39% of cells gave a maximum response to some of the stimuli used in the training. Conversely, 9% of TE cells in untrained animals responded maximally to these stimuli. These results indicate that the number of cells that respond to training stimuli increased as a result of the 1-year-long discrimination training. The spatial structure of the converted cells, as well as whether or not similar changes happened in TEO and V4, is yet to be studied.

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