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The inferior temporal cortex: Architecture, computation, and representation

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Abstract

Neurons in the inferior temporal cortex (IT), an area crucially involved in visual object recognition in monkeys, show the visual response properties and anatomical/chemical nature which are distinct from those in the cortical areas that feed visual inputs to the IT. Earlier physiological studies showed that IT neurons have large receptive fields covering the center and contralateral (often bilateral) visual fields, stimulus selectivity for images of complex objects or shapes, and translation invariance of the stimulus selectivity. Recent studies have revealed new aspects of their properties such as invariant selectivity for shapes despite drastic changes in various physical attributes of stimuli, latent excitatory inputs masked by stimulus-specific GABAergic inhibition, selectivity for binocular disparity and 3-dimensional surface structures, profound effects of learning on the stimulus selectivity, and columnar clustering of neurons with similar stimulus selectivity for shapes and other object features. Another line of research using histological techniques have revealed that pyramidal neurons in the IT are larger in the size of dendritic arbors, in the number of dendritic branches and spines, and in the size and distribution of horizontal axonal arbors than those in the earlier areas, allowing them to integrate a larger population of afferents and process more diverse inputs. The concentration of several neurochemicals including those related to synaptic transmission or plasticity changes systematically towards the IT along the occipitotemporal pathway. Many of the characteristics of IT neurons parallel or explain certain aspects of visual object perception, although the behavioral relevance has yet to be addressed experimentally.

Introduction

The inferior temporal cortex (IT) of the monkey is crucial for visual perception and recognition of objects (Gross, 1973; Ungerleider & Mishkin, 1982). The IT contains the cytoarchitectonic area TE occupying the gyral or lateral part, and the perirhinal cortex lying ventral and rostral to the TE (Fig. 1). The two areas contribute differentially to visual perception and memory. The TE is a unimodal visual area and represents the final stage for visual perceptual processing (Gross, 1973), whereas the perirhinal cortex receives polymodal sensory inputs (Suzuki, 1996a, b), and is critically involved in the formation of visual memory (Buckley *et al*., 1997; Buffalo *et al*., 1999). Dorsally, the TE adjoins cortical areas within the superior temporal sulcus (STS), which is also sometimes referred as being part of IT (*e.g.*, Baylis *et al*., 1987).

Object images are neurally represented in the IT in a manner distinct from the earlier stages that directly or indirectly provide the IT with visual information, and the manner is manifested in the physiological and anatomical characteristics of IT neurons. The first aim of this paper is to review these unique characteristics of IT neurons, and to discuss the underlying neuronal mechanism, focusing on the TE and STS cortices (for reviews on the perirhinal cortex, Miyashita, 1993; Logothetis & Sheinberg, 1996; Suzuki, 1996a). Computations performed in the TE and STS should also be reflected in, or constrained by, the anatomical structures and the spatial distribution pattern of neurons with various response properties in relation to the structural organization. Far less is known on this point compared to the primary visual cortex (V1), yet recent studies have begun to elucidate important aspects of the functional architecture of the IT. The second aim of this paper is to provide a survey of these recent developments.

Visual response properties of single neurons

LARGE AND BILATERAL RECEPTIVE FIELDS

The first single-unit recording studies of TE and STS neurons by Gross and coworkers revealed that receptive fields (RFs) of most TE and STS neurons are far larger than the neurons in the earlier cortical stages, and are generally biased to the contralateral visual field but include the fovea, and many RFs even extend into the ipsilateral field across the vertical meridian (Gross *et al*.,

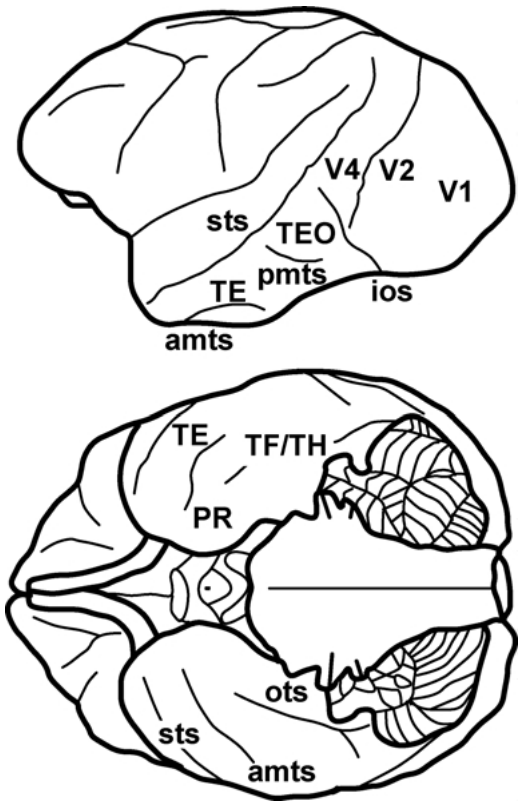

Fig. 1. Inferotemporal cortical and related areas shown in the lateral and the ventral views of the brain. amts, pmts: anterior and posterior middle temporal sulcus, ios: inferior occipital sulcus, ots: occipitotemporal sulcus, sts: superior temporal sulcus. V1, V2, V4: visual areas V1, V2, V4, PR: perirhinal cortex, TEO, TE: posterior and anterior parts of the inferior temporal visual areas, TF, TH: parahippocampal areas.

1969, 1972; Desimone & Gross, 1979; see also Tanaka *et al*., 1991; Kobatake & Tanaka, 1994). Recent quantitative measurements of RFs are in agreement with these studies, and have further shown that most RFs are regular in their spatial sensitivity, and can be fitted with Gaussian function; the response is the strongest in the RF center and gradually declines towards the periphery (Op De Beeck & Vogels, 2000; Wang *et al*., 2002). The stronger response for the RF center does not reflect selectivity for high spatial frequency in the foveal region, because the preference is preserved after extensive low-pass filtering of visual stimuli (Op De Beeck & Vogels, 2000). A small number of neurons have irregularity in their RF structure, containing either local maxima ("hotspots") or absence (a "hole") of responses within their RFs (Op De Beeck & Vogels, 2000; Wang *et al*., 2002).

All early visual areas along the occipitotemporal or "ventral" pathway (V1, V2, V4, and TEO) are organized in a retinotopic manner, albeit with different degrees of resolution, and represent the central and contralateral visual fields (Hubel & Wiesel, 1968; Gattass *et al*., 1981, 1988; Boussaoud *et al*., 1991; Van Essen & Zeki, 1978). The size of RFs at a corresponding eccentricity increases gradually with the hierarchical stages along the pathway. In the TE and STS, RFs become larger rather abruptly compared to their preceding areas, partly because RFs of many neurons extend into the ipsilateral field. Typical RFs of TE and STS neurons span 15–20 degrees of visual angle. It is sometimes claimed that TE and STS neurons essentially lose the information of stimulus position because their large RFs are overlapping among neurons and their response selectivity for visual stimuli is unchanged within the RFs. However, the above-mentioned quantitative studies show that the size of RFs varies considerably from cell to cell, and some neurons have RFs spanning only a few degrees (Op De Beeck & Vogels, 2000; Wang *et al*., 2002). Also, the center of mass of RFs is scattered within a visual field spanning ipsilateral 4 degrees to contralateral 8 degrees among neurons, raising the possibility that TE and STS neurons as a population may convey positional information within the parafoveal visual field (Op De Beeck & Vogels, 2000).

Area TE receives projections from a wide area of V4 and TEO (Desimone *et al*., 1980; Shiwa, 1987; Weller & Kaas, 1987; Weller & Steele, 1992). Divergence and convergence of these projections are thought to contribute to the enlargement of RFs in the TE (Kobatake & Tanaka, 1994). Afferent information to individual TE neurons originates from retinotopic regions beyond their RFs, and intrinsic inhibition mediated by type A receptors for γ-aminobutyric acid (GABA) in the TE shapes the RFs (Wang *et al*., 2002). All the information processed in the preceding V4 and TEO areas is not conveyed to the TE; whereas the V4 and TEO areas contain peripheral representations of 50–60 degrees in and around the occipitotemporal sulcus (Gattass *et al*., 1988; Boussaoud *et al*., 1991), only rare TE neurons have their RFs extending to this far periphery.

Many neurons in the TE respond to stimuli in the ipsilateral visual field and preserve their stimulus selectivity between the two halves of RFs across the vertical meridian (Desimone & Gross, 1979; Kawasaki *et al*., 2000). The neurons with bilateral RFs are not found in the TE of monkeys with the lesioned contralateral V1 or with both the corpus callosum and the anterior commissure sectioned (Rocha-Miranda *et al*., 1975; Gross *et al*., 1977). Preliminary experiments show that TE neurons lose responses to the ipsilateral visual field upon pharmacological inactivation of the TE on the other hemisphere (Kawasaki, K., Tamura, H. & Fujita, I., unpublished observations). These results suggest that responses to stimuli in the ipsilateral visual field depend critically on the interhemispheric projections between the right and left TEs. Because neurons with similar stimulus preferences are clustered in columnar regions in the TE (Fujita *et al*., 1992; see below), we predict that a given site on one TE should project to a particular

group of columnar regions with similar stimulus selectivity on the other hemisphere. The axons of interhemispheric projections indeed arborize in several columnar patches in layer 3 of the TE of the opposite hemisphere (Miyata *et al*., 2000).

STIMULUS PREFERENCE FOR COMPLEX STIMULI

Individual TE and STS neurons respond preferentially to particular shapes, textures or patterns, color, shapes combined with color or texture, or complex object images such as faces or objects that are used for learning or familiarization tasks (Gross *et al*., 1972; Desimone *et al*., 1984; Tanaka *et al*., 1991; Komatsu *et al*., 1992; Perrett *et al*., 1992; Booth & Rolls, 1998; Tamura & Tanaka, 2001; Sheinberg & Logothetis, 2001; Wang *et al*., 2003). Substantial populations of neurons in the V2, V4, and TEO areas respond better to shapes such as crosses and T-shapes, and to polar or hyperbolic gratings, than to bars, edges, or linear gratings (Gallant *et al*., 1993; Kobatake & Tanaka, 1994; Pasupathy & Connor, 1999; Hegdé & Van Essen, 2000). The stimuli necessary for strong activation of neurons in these areas is "simpler" than those that excite TE neurons. Object information carried by single neurons is thus transformed gradually into "complex" forms in successive areas. Except for neurons selective for faces or learned objects, however, TE neurons respond to stimuli of intermediate complexity, which are simpler than those from ordinary objects. Computational models based on units with intermediately complex selectivity have robust capability of object recognition or classification (Lowe, 2000; Ullman *et al*., 2002).

Considerable uncertainties remain about the stimulus selectivity of TE and STS neurons. First, the reported degree of response tuning markedly differs among previous studies. Some studies reported that TE and STS neurons respond more or less to all or almost all the stimuli tested (*e.g*., Desimone *et al*., 1984; Gochin *et al*., 1994), and others report that neurons respond selectively to only a small fraction of the stimuli (*e.g*., Tanaka *et al*., 1991; Fujita *et al*., 1992; Kobatake & Tanaka, 1994). This discrepancy may result from one or more of the following technical reasons. It may be due to a difference in the number and types of stimuli (novel vs. learned; geometrical figures vs. objects; within a category or across categories), a difference in the experimental protocol for characterization of neurons (the "simplification procedure" described below vs. a predetermined set of stimuli), a difference in the state of monkeys during recording (anesthetized vs. awake conditions), a difference in the animals used (naíve vs. trained or overtrained), and a difference in the recording areas (TE vs. STS or the perirhinal cortex).

Two studies have shown that tuning properties of TE neurons do not differ between anesthetized and awake conditions in adult animals (Rodman *et al*., 1991**;** Kato *et al*., 1999). The tuning curves in which the response magnitudes are plotted against stimuli in a descending order are identical between the two conditions (Kato *et al*., 1999). However, the ratio of the mean response magnitude to the response variance across trials differs between anesthetized and awake monkeys; neuronal responses to a given stimulus are more stable across trials under awake than anesthetized condition. This difference can lead to the estimation of a sharper tuning under anesthetized than awake condition, because statistical tests for responses would become more severe for TE neurons tested under anesthetized conditions.

The second uncertainty about TE and STS neuron's stimulus selectivity is both conceptual and methodological. The extreme diversity of the visual features of objects and the lack of *a priori* theory of how the brain encodes object images impede detailed characterization of the selectivity of inferior temporal neurons. A common approach is to present a predetermined set of stimuli either arbitrarily chosen from pictures of objects or scenes, or geometrical figures. In other studies, stimuli are produced mathematically (Schwartz *et al*., 1983; Richmond *et al*., 1987). In these approaches all the recorded neurons are tested with the same set of stimuli, allowing one to obtain population measures such as the average tuning width of neurons, the order of effectiveness among the stimuli tested, sparseness of the representation, the amount of information, or the population vector (*e.g*., Young & Yamane, 1992; Tovée *et al*., 1993; Rolls & Tovée, 1995; Tamura & Tanaka, 2001).

Another approach is the stimulus simplification method, which was originally performed with cut-and-paste of papers (Desimone *et al*., 1984; Tanaka *et al*., 1991) and later with computer graphics systems (Fujita *et al*., 1992; Kobatake & Tanaka, 1994; Ito *et al*., 1994, 1995; Wang *et al*., 1996; Wang *et al*., 2000, 2002, 2003). This method starts by manual presentation to a monkey of a large number (>100) of 3 dimensional objects as well as paper cutouts of various shape, color, patterns, and size. Each object is shown with different aspects, orientations, and distances. TE neurons respond strongly to a subset of objects with particular viewing conditions. Once we find the most effective stimulus for a neuron, a video image of the object is taken at its best viewing condition. We then simplify or modify the image by changing a feature singly or multiple features in combination using a computer software, present the modified images on a display under computer control, and determine the simplest stimulus configuration which activates the neuron equally well as, or more than, the original object. All these procedures are performed *on line* while the activity of the neuron is continuously monitored. An example of such procedure is shown in Figure 2. The simplest stimulus thus determined is referred to as the critical stimulus feature.

The rationale for the use of the stimulus simplification procedure is several-fold (Fujita, 1993). The first

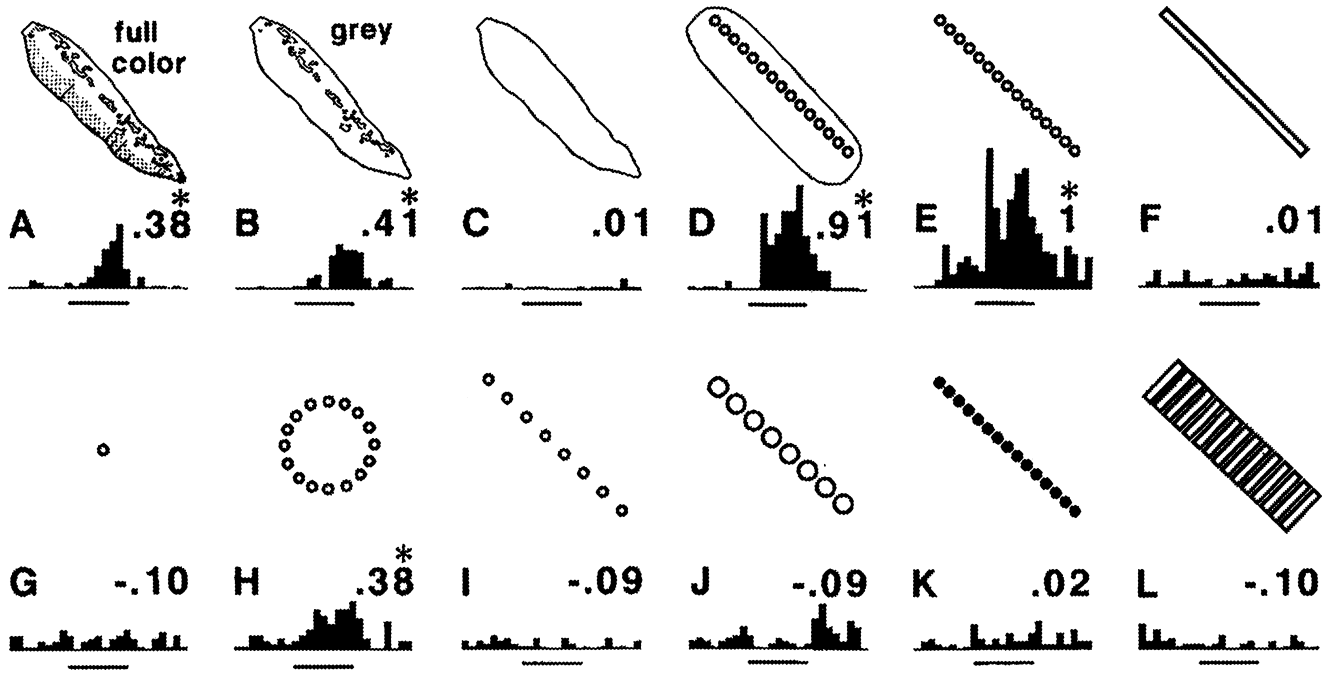

Fig. 2. Stimulus simplification procedure. In this example, a TE neuron responded to a plastic model of a carrot with conspicuous highlights on its surface. By removing or modifying component features step by step while monitoring the neuron's responses, the minimal combination of stimulus features for the strong activation of this neuron was determined as a dotted line with a leftward tilt, particular spacing and component dot size, and brighter than the background (CE). Note the stronger responses for this critical set of features than the original object (A).

and often unappreciated advantage is the initial manual presentation of a large number of objects. Because each object is shown with various aspects, orientations and distances, this could amount to a test for each neuron with more than hundreds of different visual images. Although a predetermined set of arbitrary chosen stimuli usually contain stimuli that activate TE neurons by a statistically significant amount, a careful survey in the initial phase of the stimulus simplification procedure often enables us to find more effective stimuli than those found with the predetermined set. This method represents one of the most extensive surveys for stimulus selectivity of TE neurons (see also Xiao *et al*., 2000). Second, through the simplification procedure, usually, a simpler but more effective stimulus than the original is found in the end (Tanaka *et al*., 1991). An effort is thus made to find more, if not the most, effective stimuli in this procedure. The third point is related to the nonlinearity of the stimulus selective responses of TE neurons. It is usually difficult to predict neuronal responses to complex stimuli from those to simpler ones. The simplification procedure, which starts by using a complex stimulus and proceeds to simpler stimuli, suffers less from this problem than approaches proceeding in the opposite direction.

The simplification procedure has also limitation in several ways (Young, 1993). First, the procedure is not supported by any formal theory, and performed on the basis of the experimenter's intuition. At any point of modification of a stimulus, there are a number of ways to proceed, and the experimenter chooses few of these based on his/her knowledge, hypothesis, and motivation. The search covers only a limited range of the possible modifications. Second, the simplification procedure inherently assumes that one neuron has one critical stimulus feature for its activation, but this assumption may not necessarily be warranted. Third, although the situation is better than the other approaches, the optimal stimulus thus determined for a cell is still the most effective among the stimuli tested, and may represent the local maximum of a hypersurface of high-dimensional stimulus coding space.

CODING OF BINOCULAR DISPARITY AND 3-D STRUCTURES

TE and STS neurons are selective not only for 2-dimensional shape or surface characteristics such as color or texture, but also selective for binocular disparity or binocular disparity gradient, important visual cues for perception of depth or 3-dimensional surface structure (Janssen *et al*., 1999, 2000a, b; Uka *et al*., 2000; Shimojo *et al*., 2001). All disparity selective TE neurons are selective for shape (Uka *et al*., 2000; Fig. 3). Thus, they can signal both shape and depth relative to the fixation plane. The STS contains more neurons sensitive to 3-dimensional surface structures defined by disparity gradient than the TE (Janssen *et al*., 2000b). The V4

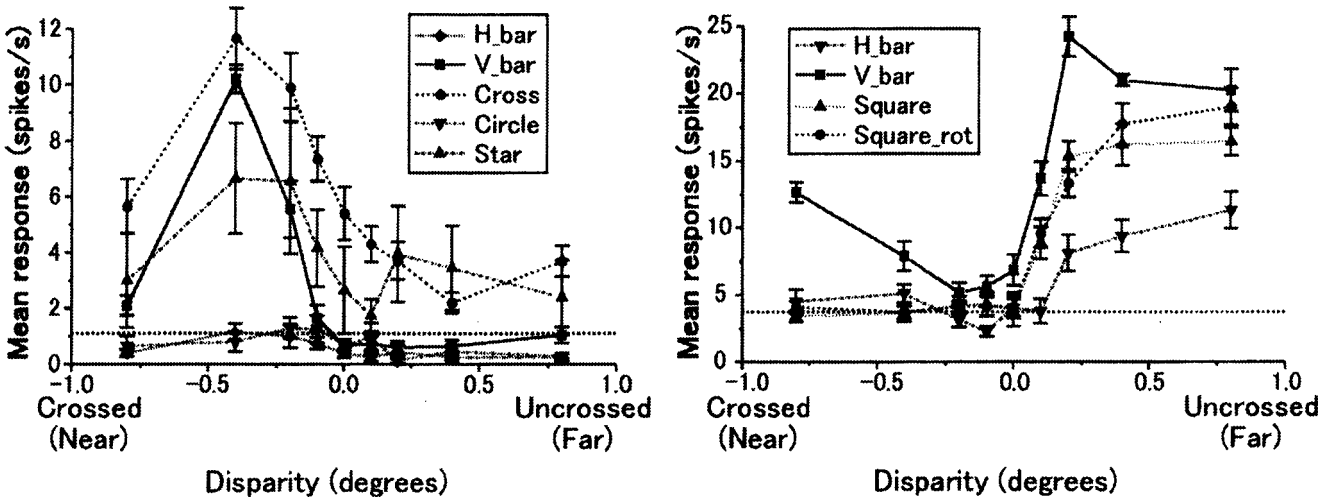

Fig. 3. Two examples of TE neurons selective for disparity. The cells are also selective for shape. H-bar, V-bar: horizontal or vertical bar, Square-rot: rotated square (diamond). Data from Uka *et al.* (2000).

area, one or two steps earlier than the TE along the occipitotemporal cortical pathway, also contains neurons selective for binocular disparity and binocular disparity gradient (Hinkle & Connor, 2001, 2002; Watanabe *et al.*, 2002). On the other hand, neurons in the posterior parietal cortex have been recently shown to respond to 2-dimensional shapes (Sereno & Maunsell, 1998). These new findings indicate that the functional dichotomy between the occipitoparietal visual pathway and the occipitotemporal visual pathway (Ungerleider & Mishkin, 1982) does not hold to the extent that the two pathways process distinct sets of visual attributes. The findings raise the question of which area(s) is (are) responsible for stereopsis, and if multiple areas are involved, whether there is a division of labor between them.

RESPONSE INVARIANCE

A remarkable feature of TE and STS neurons is invariance of shape selectivity despite a drastic transformation of stimuli (Vogels & Orban, 1996). Preference for a particular shape over others is preserved in many neurons, when the stimulus is placed in different positions within the RF (Gross & Mishkin, 1977; Schwartz *et al.*, 1983; Tovée *et al.*, 1994; Lueschow *et al.*, 1994; Ito *et al.*, 1995), when the defining cues of shapes are changed between luminance, texture, motion, and binocular disparity (Sáry *et al.*, 1995; Tanaka *et al.*, 2001) or when shapes are partially occluded (Kovács *et al.*, 1995). Stimulus selectivity is also preserved when neurons are tested under more natural viewing conditions such as in the presence of background or during a search by free viewing for targets in a cluttered scene (Missal *et al.*, 1997; DiCalro & Maunsell, 2000; Sheinberg & Logothetis, 2001). Note, however, that the response magnitude will often change after these transformations. Changes in the size and contrast polarity lead to different effects on different neurons; shape selectivity of some neurons is invariant to changes of size and contrast polarity, while other neurons alter their shape selectivity by these changes (Ito *et al.*, 1994; but see Rolls & Baylis, 1986). TE neurons are generally sensitive to changes in orientation of shapes (Tanaka *et al.*, 1991). Interestingly, selectivity is less affected by mirror reversal than by upside-down reversal or by figure-ground reversal (Rollenhagen & Olson, 2000; Baylis & Driver, 2001).

These physiological properties are strikingly consistent with visual perceptual performance by human subjects in the following aspects. We can generally recognize objects regardless of changes in their position, distances (hence, retinal size), and defining cue. Psychological and theoretical studies suggest that shapes are processed and stored in a size-specific manner under certain conditions (Jolicoeur, 1987; Ullman, 1989). Children more often make mirror-reversal mistakes than upside down mistakes in writing and reading letters (such as b and d vs. b and p); a similar situation exists for Japanese children in writing Japanese ("Kana") letters. Finally figure-ground reversal influences our perception of many figures.

SHAPING STIMULUS SELECTIVITY

It was previously proposed that stimulus selectivity for complex shapes is created in the V4 and TEO areas, and is conveyed to the TE (Kobatake & Tanaka, 1994; Tanaka, 1996). Recent studies have shown that the process of shaping the stimulus selectivity continues in the TE, and that inhibition mediated by $GABA_A$ receptors contributes to this process. Approximately a quarter of neurons in area TE are inhibitory interneurons that contain GABA (Hendry *et al.*, 1987). Removal of GABAergic inhibition by local application of bicuculline methiodide, a $GABA_A$ receptor antagonist, in

the vicinity of a TE neuron markedly alters its stimulus-selective responses (Wang *et al*., 2000, 2002, 2003). Bicuculline application augments responses to some stimuli or even unmasks responses to stimuli that did not elicit responses before, while responses to others, including some of the originally effective stimuli, are unaffected. The effects are observed for particular groups of stimuli, which include those related to the originally effective stimuli and those that do not originally excite the neurons but activated nearby neurons. The change in the responses cannot be accounted for either by a "gain effect" (*i.e*., multiplicative enhancement of responses to all stimuli) or by an "iceberg effect" (*i.e*., enhancement by the same amount of responses to all stimuli). TE neurons appear to receive inputs on diverse stimuli, part of which is selectively suppressed by GABAergic inhibition in the TE.

Stimulus-specific inhibition does not necessarily require inhibitory neurons with stimulus-specific responses. It can occur if inhibitory neurons with poor stimulus tuning can exert shunting or "short-circuiting" inhibition on particular dendrites that receive stimulus-specific excitatory inputs. Conversely, broadband inhibition can be mediated by stimulus-selective inhibitory interneurons, if inhibitory neurons selective for different stimuli converge onto the same postsynaptic neuron. Recent experiments with multiunit recordings have identified inhibitory interneurons by applying cross-correlation analysis to simultaneously recorded TE neurons, and have shown that presumed inhibitory neurons are as stimulus selective as excitatory TE neurons (Tamura *et al*., 2003). Inhibitory interactions more frequently occur in pairs with less similar stimulus preferences than those with more similar stimulus preferences. These observations are consistent with the results of the bicuculline experiments and suggest that inhibitory TE neurons shape the stimulus preferences of their target TE neurons through stimulus-specific inhibition.

Existence of neurons in the TE, STS, and the perirhinal cortex responding selectively to a complex object used in a behavioral task has made researchers suspect that selectivity of these neurons is created by training the monkeys. Accumulating evidence indicates that neurons in these areas indeed change their stimulus selectivity through learning (for reviews, see Miyashita, 1993; Logothetis & Sheinberg, 1996; For recent works, see Kobatake *et al*., 1998; Baker *et al*., 2002; Sigala & Logothetis, 2002). The effects appear to be more robust in the perirhinal cortex or the ventral part of the TE than in the dorsal TE and the STS. Depending on whether learning effects involve the tuning mechanism or association mechanism (Desimone, 1992), the selectivity of neurons can become sharper or broader. Both mechanisms among others occur in the TE and the perirhinal cortex.

Functional and anatomical architecture

COLUMNAR ORGANIZATION

Neurons responding to similar stimuli or those with correlated stimulus selectivity cluster locally within the TE (Gochin *et al*., 1991; Fujita *et al*., 1992; Gawne & Richmond, 1993). These clusters are columnar in shape; neurons with shared stimulus preferences are arrayed vertically across the cortical layers, but are localized within a range of 0.4–0.5 mm across the cortical surface (Fujita *et al*., 1992). Experiments from tangential penetrations suggest that there are multiple columns responding to similar stimuli with an interval of 0.4–1 mm between them (Fig. 4). The number of columns in the TE on one hemisphere is estimated to be 1300–2000. The evidence for the columnar organization is available from single-unit recordings (Fujita *et al*., 1992; Wang *et al*., 2000) and optical imaging (Wang *et al*., 1996; Tsunoda *et al*., 2001) in anesthetized monkeys and from single-unit recordings in awake, fixating monkeys (Fujita *et al*., 1996; Kato *et al*., 1998).

Neurons in a TE column are not identical, though similar or correlated, to each other in their stimulus selectivity. We noted this in our initial study, where we employed the simplification procedure (Fujita *et al*., 1992). Later studies tested responses of TE neurons with a fixed stimulus set and estimated the similarity of selectivity by calculating correlation coefficients between responses of two neurons. The correlation is higher for neuronal pairs recorded at the same site or in the same penetration than those recorded in different penetrations, supporting the notion of columns in the TE (Gochin *et al*., 1991; Gawne & Richmond, 1993; Kato *et al*., 1998; Wang *et al*., 2000). When we compare different studies, the mean correlation coefficient for nearby

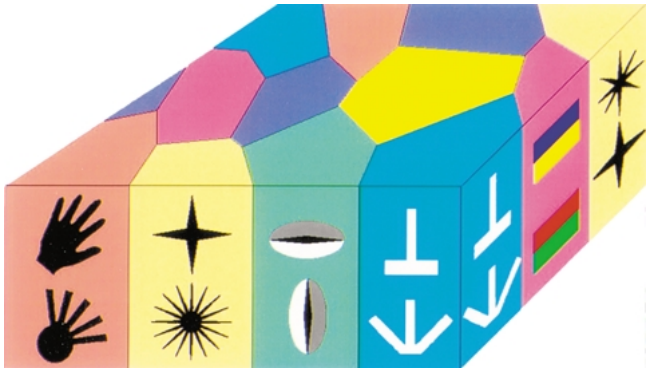

Fig. 4. A schematic drawing of the functional columnar organization of the TE. Neurons within a column respond to the same or a similar stimuli, but the exact optimal stimulus or the tuning properties differ among them, as exemplified by similar but different icons within each column. Multiple columns are selective for similar features, and are shown with the same color.

cells varies considerably among them. Although the absolute value of the correlation coefficient depends on the stimulus set and is difficult to interpret, there is a tendency that studies employing an arbitrary set of stimuli yield lower coefficient values. In studies where the stimulus set contained the critical stimulus feature determined for the tested region by the prior stimulus simplification procedure, the mean of the correlation coefficient for the same penetration was as high as 0.30 (Fujita *et al*., 1996) or 0.35 (Wang *et al*., 2000).

It is unclear how columns responding to different object features are arranged in the TE. Despite intense efforts in several laboratories, no convincing evidence is available suggesting that any particular features or parameters are continuously represented across the cortical surface in the TE. This may not be surprising, because mapping of the vastly high dimensional information about object features onto the 2-dimensional cortical sheet would inevitably invoke many discontinuities (Young, 1993), and because representation of objects is likely to involve processing of information locally and distantly separated in the stimulus space, for which patchy mapping of information onto the cortex may be more advantageous than continuous mapping (Nelson & Bower, 1990). Also, no evidence is available suggesting that neurons are arranged according to a particular rule within a column. An exception may be columns responding to a face where different views of a face activate slightly shifted but overlapping regions (Wang *et al*., 1996).

The columnar organization of the TE suggests that when a monkey sees an object, a particular group of columns will be activated by the image, because an ordinary object is rich in features, different features of an object will activate different columns, and each feature may activate multiple columns (see above; Fujita, 1993). Optical imaging experiments confirmed this prediction, showing that an object activate multiple spots of regions over the TE surface, and parsing and simplifying images gradually decrease the number of activated spots (Wang *et al*., 1996; Tsunoda *et al*., 2001). Simplifying the original image sometimes leads to the appearance of new spots that are not originally activated. This may imply that the representation of an object cannot simply be viewed as a combination of active columns but we should consider inactive columns as a part of the representation, as Tsunoda *et al*. (2001) suggested. Alternatively, new spots may be activated by a new feature inadvertently introduced in the simplified image.

We previously proposed a hypothesis ("visual alphabet hypothesis") about how the TE columns represent objects (Fujita *et al*., 1992; Fujita, 1993; Tanaka, 1996; see also Stryker, 1992). In this scheme, we hypothesize that individual columns encode particular object features to which output neurons in the respective columns respond. Since different objects contain different combinations of features, which activate different subsets of columns, the combination of active columns can in principle specify the whole object. As the 26 alphabets in English produce a million of words, 1300–2000 columns in the TE can represent an enormous variety of objects by virtue of combination of intermediately complex features. Unlike phonetic symbols such as the alphabets, however, the features represented in columns are not an arbitrary set of elements, but are likely to be constrained by the statistics in the structure of the natural scenes. It is noteworthy that we encounter columns of neurons responding to T- or L-shapes or those responding to gradual changes of luminosity across animals.

The visual alphabet hypothesis thus postulates that a large number of TE neurons is engaged in representation of an object, but this is not a population coding in the sense of DeCharms and Zador (2000). They distinguish a population coding in which information is explicit only in the relation among activities of multiple neurons and not encoded by individual neurons (as a symphony played by an orchestra) from a coding scheme where information is explicit in activity of individual members of an ensemble (as a voter's opinion in an election). In an orchestra, different instruments play together and create a synergy effect that any of the instruments alone cannot produce. In an election, the result of the election depends on the entire voters, but each voter can express his/her own opinion independently of others. A combinatorial coding such as the visual alphabet hypothesis in its simplest form is similar to the latter coding scheme in the sense that each column represents a particular feature.

Given the diversity of selectivity across neurons in a column, however, activities in each column can signal more than "yes" or "no" regarding the presence of a particular feature in an object, and therefore, activities across neurons within a column can form a population code. A change in a visual feature due to change in the viewing conditions, for example, may activate overlapping but different patterns of activation across neurons in a column or multiple columns that are sensitive to that feature. The activity pattern across neurons can thus signal changes in visual images, while keeping the representation of identity of objects (Fujita *et al*., 1992; Fujita, 1995; Wang *et al*., 1996).

As a final remark on the columnar organization, TE neurons also cluster locally according to their disparity selectivity (Uka *et al*., 2000; Yoshiyama *et al*., 2000). Neurons recorded at a site with a single electrode tend to share the preferred disparity and the ability of disparity discrimination. It remains to be determined how this disparity cluster is spatially related to columns defined by selectivity for shape.

INTRINSIC FIBER CONNECTIONS

The TE and other cortices share some of the basic patterns of the intrinsic fiber connection. For example,

extensive vertical interlaminar connections exist; cells in layer 3 project heavily to layer 5, and cells in layers 4–6 ascend to layer 3 (Fujita & Fujita, 1996). Another feature common to the TE and other cortices is horizontal axons originating from pyramidal cells and running parallel to the pia mater. Horizontally running axons can be observed in all layers. Those in layers 2 and 3 run for the longest length (4–8 mm), and produce distinct plexuses of terminal arborization (horizontal axonal "patches") at intervals (Fujita & Fujita, 1996; Tanigawa *et al*., 1998). These axonal terminal patches are columnar in shape along the plane perpendicular to the surface. Axons and terminal boutons are mainly distributed from layer 1 to 3, and sometimes found from layer 1 to 5. Each patch measures 0.35–0.4 mm wide on average, which roughly coincides with the size of a functional column estimated in physiological experiments. The distance between columns responding to the same or similar stimuli (0.4–1.0 mm) is also comparable to the range of distances between horizontal axonal patches. Terminal arborization of afferent fibers from the TEO (Saleem *et al*., 1993) and from the contralateral TE (Miyata *et al*., 2000) also takes a columnar form of similar size in the TE. All these anatomical features make extensive interactions across layers possible and provide common inputs to cylindrical regions of the cortex, thus contributing to the shared stimulus selectivity among neurons within a column.

The topographic features of horizontal axon patches markedly differ between V1 and TE (Fig. 5; Tanigawa & Fujita, 1997). Patches of axonal arbors in the TE are larger, more widely spaced, and more irregularly distributed than those in V1. When we label horizontal axons by injecting an anterograde neuronal tracer, the labeling intensity of patches gradually declines with increasing injection-to-patch distance in V1, but this tendency is less apparent in the TE. This suggests that horizontal axons in V1 link nearby cortical sites more strongly than distant sites, but the connection by horizontal axons in TE depends less on the distance between the two sites. When two different anterograde tracers are focally administered into a pair of adjacent sites abutting each other, most of the clusters produced by the two injections neither overlap nor abut each other, although in one or two of the clusters, projections from the two injections overlap partially or extensively (Tanigawa & Fujita, 1997). This indicates that adjacent sites in the TE are largely connected to spatially distinct sets of sites via horizontal axons. Given the extensive fiber connections through recurrent axon collaterals between neighboring sites, the organization of the TE increases the opportunity for interaction among columns which are selective for different object features, compared to an organization in which adjacent columns project to adjacent sites. The findings, taken together, suggest that the TE is an example of patchy brain map, whereas V1 represents a continuous brain map of Nelson and Bower (1990).

The differences in horizontal axonal patches between the TE and V1 already exist in animals injected with a tracer on the postnatal day 3 and perfused on day 7. Patches with area-specific topographic features are formed early in life, presumably *in utero*. Prolonged, area-specific changes, however, appear to occur within patches after birth, and refine the two areas into their adult organization (Wang *et al*., 1998).

The size, center-to-center spacing, and spread of horizontal axon patches in areas V2 and V4 are intermediate between V1 and the TE, and thus there is a gradual change in these parameters along the occipitotemporal

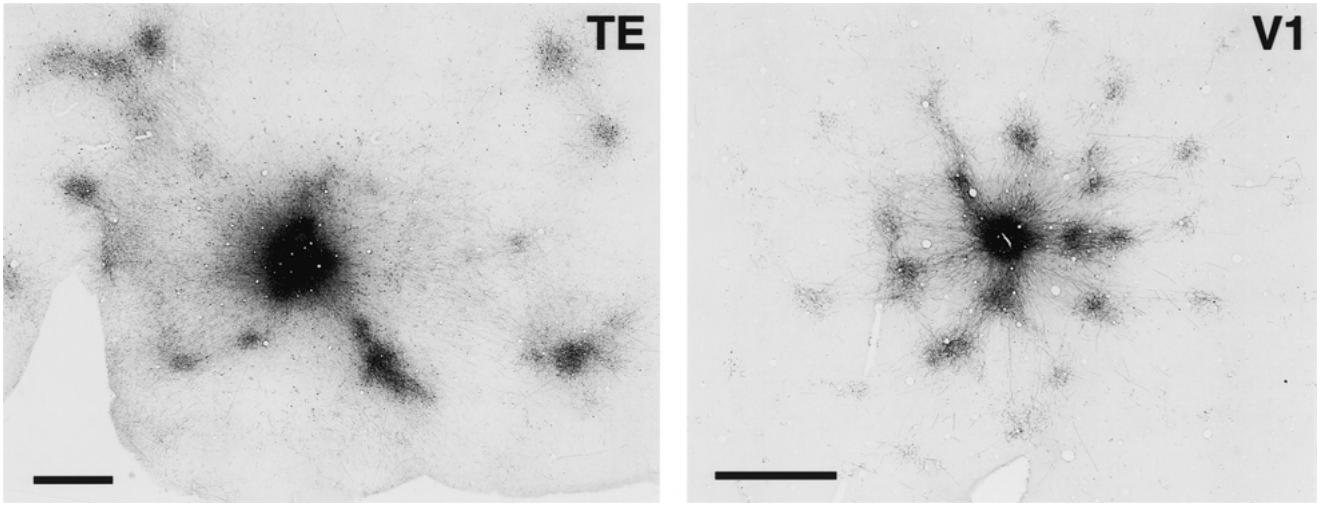

Fig. 5. Striking differences in the topographic features of intrinsic horizontal axons in the TE and V1. An anterograde tracer, biotinylated dextran amine, was injected into the TE and V1, and labeled axons and terminals were visualized with DAB reaction. Scale bars: 1 mm.

pathway (Yoshioka *et al*., 1992; Amir *et al*., 1993; Lund *et al*., 1993). Also, the tangential spread of the basal dendrites and the number of dendritic branches and spines of pyramidal neurons in layers III and V increase along the pathway (Lund *et al*., 1993; Elston & Rosa, 1998, 2000; Elston, 2003). These morphological characteristics may allow the neurons of later stages in the pathway, particularly in the TE, to integrate information from larger population of afferent neurons and/or larger visual fields (Amir *et al*., 1993; Elston & Rosa, 1998, 2000; Elston, 2003). These morphological characteristics may produce fundamental and systematic differences in the size and diversity of inputs delivered to or sampled by a single neuron among different cortical areas.

Intrinsic horizontal axons enable distant sites within a cortical area to interact with each other. Horizontal axons in the TE are not for interactions between neurons responding to different parts of the visual field as proposed for V1, considering that TE neurons have largely overlapping RFs with each other. It is likely that the connections are related to the stimulus selectivity of columns. It is an open question whether horizontal axons connect columns responding to similar stimuli, different stimuli, or stimuli that occur together more often than the others due to the high correlational structure of the visual world.

High-frequency electrical stimulation of horizontal axons in layers 2 and 3 evokes contrasting forms of synaptic plasticity in the TE and V1 (Murayama *et al*., 1997). It causes long-term potentiation (LTP) of synaptic transmission efficacy mediated by this axon system in the TE. In V1, an identical stimulus protocol produces long-term depression (LTD) in the same fiber system. Visual areas belonging to the same functional pathway thus have different susceptibility to synaptic plasticity (Fujita *et al*., 1996; Murayama *et al*., 1997). The mechanism underlying this difference is unknown; it may be due to differences in biophysical membrane properties of neurons between the TE and V1, structural differences between the two areas, or the differences in the distribution of neurochemicals regulating LTP/LTD between them (see below).

NEUROCHEMICAL CHARACTERISTICS

In addition to the gradual changes in structure, there exist also changes in the distribution of neurochemicals including those related to synaptic transmission and plasticity along the occipitotemporal pathway. Concentration of a subtype (μ-like) of opiate receptors (Lewis *et al*., 1981), phosphorylation levels of the substrates of protein kinase C (protein F1 and a 81 kDa protein; Nelson *et al*., 1987), the number of calbindin-immunoreactive pyramidal cells (Kondo *et al*., 1994), and immunoreactivity for AMPA-type glutamate receptor subunits (GluR2/3) (Xu *et al*., 2003) gradually increase towards the anterior portion of the pathway. Parvalbumin immunoreactivity shows an opposite gradient, being the strongest in V1 and gradually decreasing in more anterior areas along the pathway (Kondo *et al*., 1994). The *occ1* gene, encoding a macaque homologue of TSC-36/follistatin-related protein, shows a strikingly strong expression in V1 but weak or undetectable expression in the anterior cortical areas (Tochitani *et al*., 2001).

Conclusion

Studies in the past decade have revealed new aspects of response properties and structural characteristics of TE and STS neurons, many of which explain the computations proposed to occur in these areas or parallel our visual perception. Relating physiological findings obtained in monkeys to psychological phenomena in human subjects will continue to yield important insights on the function of the inferior temporal cortex. However, the most direct evidence for functional roles of a given cortical pathway, an area, a population of neurons, or a single neuron will of course come from behavioral and physiological studies conducted in the same species or in the same individual. Noninvasive functional imaging of the human brain during a perceptual task is one such approach with a limitation of spatial and temporal resolution. There are many other methodological approaches to address the behavioral relevance of a given neuronal activity in animal experiments (Parker & Newsome, 1998), although only few attempts have been made on the TE and STS. An example is the demonstration of a close correlation between the response of face selective neurons in the STS and the animal's report of perceiving a face during binocular rivalry condition (Sheinberg & Logothetis, 1997). Behavioral relevance of the various response properties of TE and STS neurons reviewed in this article should be experimentally addressed in future studies.

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