Inferotemporal Cortex: A Single-Unit Analysis

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ABSTRACT Inferotemporal cortex, the cortex on the inferior surface of the primate temporal lobe, is involved in complex visual functions. Neurons in inferotemporal cortex respond only to visual stimuli and have large receptive fields that always include the center of gaze and often extend into both visual half-fields. Most neurons were sensitive to the size, shape, orientation, or direction of movement of the stimulus. Their visual responsiveness was dependent on input from striate cortex but not on input from the pulvinar. Inferotemporal cortex appears to extend the feature-detecting mechanisms found in the geniculo-striate system and may have additional functions.

Little is known of the neuronal mechanisms underlying perception, cognition, and memory: There is still an enormous gap between the phenomena of human consciousness and our knowledge of neuron physiology. The study of inferotemporal cortex may provide an opportunity for reducing this gap. Inferotemporal cortex is "association cortex" on the inferior convexity of the primate temporal lobe (Figure 1A); its removal produces a specifically visual cognitive disorder. Since inferotemporal cortex receives afferents from several visual areas and sends efferents both to other association cortices and to various limbic structures, an understanding of its functions should provide a bridge between sensory physiology and the physiology of cognition.

In many parts of the success of single neuron recording in analyzing other cortical areas, we set out to explore inferotemporal cortex at the neuronal level. The first part of this essay outlines the problem by summarizing the behavioral effects of inferotemporal lesions and the anatomic relations of inferotemporal cortex with other brain structures. In the second part, we describe our experiments on the response properties of neurons in inferotemporal cortex (Gross et al., 1967, 1969, 1972). The third part is devoted to our experiments on the anatomical pathways that contribute to these properties (Bender et al., 1972).

The problem

Both the behavioral effects of inferotemporal lesions and the anatomical connections of inferotemporal cortex provide some clues to the functions of this tissue.

In monkeys bilateral inferotemporal lesions produce a severe deficit in visual discrimination performance. After such lesions, monkeys are impaired in the retention and acquisition of visual discrimination tasks involving pattern, brightness, or color cues. (See reviews by Pribram, 1967; Gross, 1972a, b; Mishkin, 1966.) This deficit is specific to vision; learning in other modalities remains normal. However, inferotemporal lesions do not affect basic visual functions such as visual acuity, visual perimetry, backward masking, and several psychophysical thresholds (Cowey, and Weiskrantz, 1967; Gross, 1972b). A similar loss of visual recognition and visual memory follows lesions of the temporal cortex of the nondominant hemisphere in man (Milner, 1968). Thus, in man and monkey, inferotemporal cortex appears to be involved in higher order perceptual and cognitive processes underlying visual recognition.

Inferotemporal cortex receives afferents from two areas that process visual information. The first is the circumsstriate belt, which in turn receives projections from striate cortex (Figures 1A and 2). Hubel and Wiesel have proposed a hierarchy of visual feature detectors extending through the geniculo-striate system into the circumsstriate belt (Hubel and Wiesel, 1962, 1965, 1968, 1970). The projection of the circumsstriate belt onto inferotemporal cortex suggests that inferotemporal cortex may be a further stage in this hierarchy. A second source of visual information for inferotemporal cortex is the projection it receives from the pulvinar. The pulvinar, in turn, receives a projection from the superior colliculus (Figure 2). The superior colliculus and perhaps the pulvinar are involved in visual orientating and localizing functions (Denny-Brown and Chambers, 1958; Schneider, 1969; Schiller and Koerner, 1971; Goldberg and Wurtz, 1972; Humphrey, 1970). Thus, inferotemporal cortex may integrate the orienting mechanisms of a tecto-pulvinar
system with the feature detection mechanisms of the geniculo-striate-circumstriate system.

Inferotemporal cortex sends outputs to limbic structures such as the amygdala, entorhinal cortex, and hippocampus, which are thought to be involved in motivational and mnemonic aspects of behavior (Figure 2). These connections suggest that inferotemporal cortex might also play a role in the storage and retrieval of visual information and in giving it gnostic significance (see Weiskrantz, 1970). This possibility is supported by the behavioral analysis of the inferotemporal deficit. The deficit depends not only on the visual discrimina nda but also on several nonsensory factors such as the animal's prior experience, the training procedure used, and the type of reinforcement (Gross, 1972a, b).

In summary, the effects of inferotemporal lesions and the connections of inferotemporal cortex indicate that this cortex plays a unique and integrative role in visual pattern recognition.

Visual properties of inferotemporal neurons

Our methods have been described in detail elsewhere (Gross et al., 1972). Monkeys were anesthetized with a mixture of nitrous oxide and oxygen, paralyzed to eliminate eye movements, and artificially respired. Their eyes were focused on a 64° × 64° tangent screen onto which visual stimuli were projected. Discharges of isolated neurons were recorded with platinum-iridium electrodes and displayed on an oscilloscope, played over a loudspeaker, recorded on magnetic tape, and analyzed with a PDP-12 computer. The computer was also used to control the presentation of the visual stimuli on the screen.

Modal Specificity and Latency All the neurons we encountered were spontaneously active. We were able to drive about three-quarters of them with visual stimuli, whereas none were responsive to a variety of auditory, somesthetic, and olfactory stimuli. This demonstration

Figure 1 (A) Diagram of lateral view of cerebral hemisphere of Macaca mulatta. The circumstriate belt is shown after Kuypers et al. (1965). In this chapter "circumstriate belt" and "pre-striate cortex" are used synonymously. Inferotemporal cortex is defined as corresponding to von Bonin and Bailey's (1947) area TE. The vertical line indicates the level of the coronal section shown in B. (B) Coronal section through the temporal lobe. The arrow shows the site of entry of a typical pass and the dots indicate the approximate location of representative cells recorded on that pass. (C) Receptive fields of the inferotemporal neurons whose locations are shown in B. The receptive fields recorded at increasing depth are shown from left to right starting at the top left. The axes represent the horizontal and vertical meridia of the visual field, and the half-field contralateral to the recording electrode is on the left. The scale is in degrees of visual angle. Note that all receptive fields include the fovea and that some extend well into both visual half-fields. INTRAPAR. S. = intraparietal sulcus; PRINC. S. = principal sulcus; LAT. F. = lateral fissure; SUP. TEM. S. = superior temporal sulcus; INF. OCC. S. = inferior occipital sulcus; Cd = caudate nucleus; H = hippocampus; PI = pulvinar; TE (inferotemporal cortex), TA, TF and TH refer to cytoarchitectonic areas of von Bonin and Bailey.
that inferotemporal neurons respond only to visual stimuli parallels the previous findings that inferotemporal lesions impair only visual learning.

The response latency of inferotemporal neurons to visual stimuli was surprisingly long. No neurons responded before 70 msec, and the mean latency of the earliest part of the response was about 120 msec (Figure 3). In many units, time-locked activity continued for 400 msec or longer after the stimulus offset.

**Figure 3** Poststimulus time histogram for a unit in inferotemporal cortex. The stimulus was a vertical 1° × 70° black slit centered on the fovea. It was presented twenty times for a duration of one second with an interstimulus interval of 10 sec. The horizontal line indicates the stimulus duration. The vertical scale indicates total impulses per bin. The bin width was 15.6 msec. The long latency of the response was typical of inferotemporal neurons.

**Receptive Fields** The activity of almost all neurons was altered only by stimulation of a restricted portion of the visual field; i.e., the neurons had "receptive fields." Every receptive field included the center of gaze, the fovea. Over half of the receptive fields extended well into both visual half-fields, about one-third were in the half-field contralateral to the electrode, and the rest were in the ipsilateral half-field (Figures 1C, 4, and 5A). This is in striking contrast to the geniculostriate system in which the receptive fields are confined, within a few degrees, to the contralateral half-field and do not invariably include the center of gaze (e.g., Hubel and Wiesel, 1960, 1965, 1968). Another unusual feature of the inferotemporal receptive fields was their large size. They were usually more than 10° × 10° with a median area of 418 square degrees and an interquartile range of 150 to 1410 square degrees, (Figures 1C and 4).

**Effects of Stimulus Parameters** The strength of a response or even its existence was usually dependent on several parameters of the stimulus. Among these parameters were contrast, wavelength, size, shape, orientation, and direction of movement. Some neurons were
sensitive to all of these parameters, whereas other neurons were sensitive to only a few. Most neurons responded more vigorously to a moving stimulus than a stationary one. About three-quarters of the responsive neurons could be driven by dark stimuli on a white background, about three-quarters by light stimuli on a dark background, and about half of them were responsive to both contrast conditions. For the great majority of neurons, a white, black, or colored slit about 1° in width was a more potent stimulus than other rectangular or circular stimuli. About half of the units were sensitive to the orientation of the slit. Of these, some responded best or exclusively to one direction of movement of the slit in its optimal orientation while other neurons responded...
equally well to both directions of movement, e.g. Figure 4. We found a number of neurons that were more responsive to a colored stimulus than to a white stimulus presented over a great range of intensities. Red sensitive neurons were far more common than either blue or green ones. The optimal stimulus or trigger feature for a cell was optimal throughout the entire receptive field, although stimulation of the receptive field at the fovea usually produced the most vigorous response.

A minority of the cells we studied had extremely specific and complex trigger features, most of which were discovered accidentally. Among such neurons were ones whose best stimulus appeared to be a monkey hand, the shadow of a hemostat, a bottle brush, or a specific curvature. Some of these neurons responded more vigorously to a particular three-dimensional object than to any two-dimensional representation of it. It is possible, of course, that some of the apparently nonspecific neurons in our sample actually had highly specific trigger features that we never found. That is, a neuron that responded best to a 1° x 5° red slit oriented at 45° within its receptive field may not have been coding this size, shape, color, and orientation. Rather, its trigger feature might have been a far more specific, complex, and perhaps meaningful stimulus that we never used and that happened to share some of the stimulus parameters of the stimulus we did use.

In summary, we found that neurons in inferotemporal cortex were exclusively visual and had large receptive fields that always included the fovea and often extended into both visual half-fields. They coded (i.e., differentially responded to) many aspects of the stimulus and some of them had highly specific trigger features.

**Functional anatomy**

**Afferent Connections of Inferotemporal Cortex**

How do neurons in inferotemporal cortex receive the visual information that is the basis of their visual properties? Inferotemporal cortex receives projections from both the circumstriate belt (Kuypers et al., 1965; Jones, and Powell, 1970) and from the pulvinar (Chow, 1950). Both these structures are known to process visual information, and both, in turn, receive projections from visual areas that have been well studied.

Striate cortex projects to at least three areas of the circumstriate belt, which Zeki has named V2, V3, and the “posterior superior temporal sulcus field” (Zeki 1969, 1971a, b; Cragg and Ainsworth, 1969; Cowey, personal communication). These projections appear to be retinotopically organized. Both V2 and V3 project to the same posterior superior temporal area to which striate cortex projects and also to three regions in the anterior portion of the circumstriate belt, two of these Zeki has designated V4 and V4A, and the third may be called V5 (Zeki, 1971b; Cowey, personal communication). Retinotopic organization, at least anatomically, is no longer discernable in V4, V4A, and V5. Finally, areas V4, V4A, and V5 project in a diffuse fashion to inferotemporal cortex (Cowey, personal communication). There are extensive interhemispheric connections between the circumstriate belts carried by the splenium of the corpus callosum (Zeki, 1970; Pandya et al., 1971). These interhemispheric connections could bring representations of the ipsilateral visual field to each hemisphere. Thus, each inferotemporal cortex could receive visual information about the entire visual field from striate cortex by way of a minimum of two synapses in the circumstriate belt. However, the long latency of the visual responses of inferotemporal neurons suggests that there is more processing in the circumstriate belt than this minimum of two synapses implies. Perhaps prior to its arrival in inferotemporal cortex, there is considerable recycling of visual information (see Barlow et al., 1972).

In addition to this corticocortical input, inferotemporal cortex also receives a projection from the pulvinar (Chow, 1950). Neurons in the inferior pulvinar are responsive to visual stimuli, and a retinotopic organization of this area has been described (Allman et al., 1972). The inferior pulvinar, in turn, receives projections both from striate cortex (Myers, 1962) and the superior colliculus (Mishkin, 1972; Mathers, 1971). Thus, inferotemporal cortex could also receive visual information by way of synapses in the pulvinar from either striate cortex or the superior colliculus. The afferent and efferent connections of inferotemporal cortex are summarized in Figure 2.

**Functions of the Afferents to Inferotemporal Cortex**

What are the functional roles of the cortical and subcortical projections to inferotemporal cortex? Normal visual pattern discrimination learning is dependent on the input to inferotemporal cortex from striate cortex by way of synapses in the circumstriate belt. Direct or indirect interruption of this corticocortical pathway or of its foveal component produces a deficit in visual learning at least as severe as that after inferotemporal lesions (Mishkin, 1966, 1972; Cowey, and Gross, 1970). By contrast, destruction of the pulvinar does not impair visual pattern learning (Chow, 1954; Mishkin, 1972).

In three experiments we directly studied the contribution of the afferent pathways to inferotemporal cortex (Bender et al., 1972). In the first experiment, we totally removed the striate cortex of one hemisphere in several monkeys. If the visual properties of inferotemporal cortex were dependent on striate cortex, then after unilateral ablation of striate cortex inferotemporal units should have been responsive only to visual stimulation in the half-field contralateral to the remaining striate cortex (Figure 5).
Figure 5

Figure 6

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This hypothesis was confirmed: In the animals with unilateral striate lesions, all the receptive fields in both inferotemporal cortices were unilateral and confined to the visual half-field contralateral to the intact striate cortex, whereas in normal animals the majority of receptive fields had extended well into both visual half-fields (see Figures 5A, 5C, 5D, and 6B).

In the second experiment, the corpus callosum and anterior commissure were sectioned. If these interhemispheric connections were the basis of the responses to stimulation in the ipsilateral half-field that characterized two-thirds of the inferotemporal neurons, then sections of these connections should eliminate such responses. This hypothesis was also confirmed as shown in Figure 5B and 6A.

Although these experiments demonstrated that inferotemporal cortex receives visual information from striate cortex, they did not establish the specific route, except that it must include the corpus callosum or anterior commissure. As shown in Figure 2, inferotemporal cortex could receive input from striate cortex either by way of synapses in the circumstriate belt or by way of synapses in the pulvinar (the pulvinar route could also involve the superior colliculus, the circumstriate belt, or both areas).

In the third experiment, we studied the effects of bilateral pulvinar lesions to decide between a corticocortical route and a route involving the pulvinar. After pulvinar lesions, we found the incidence of responsive neurons in inferotemporal cortex and their trigger features to be the same as those in intact monkeys. There was, however, a dramatic and unexpected effect of the pulvinar lesions: Virtually none of the inferotemporal neurons had discrete receptive fields; rather, they responded to visual stimulation throughout the 64° x 64° area of the tangent screen on which the visual stimuli were projected (see Figure 7). Thus the receptive field boundaries of inferotemporal neurons appear dependent on the input from the pulvinar, whereas their trigger features are dependent on the corticocortical input.

The devastating effects of interrupting the corticocortical pathway from striate cortex to inferotemporal cortex, both on the visual properties of inferotemporal neurons and on the performance of visual discrimination tasks, indicate the crucial nature of this pathway for the functioning of inferotemporal cortex. The topography of this multisynaptic pathway suggests explanations for two unusual properties of inferotemporal neurons. The invariable inclusion of the fovea in the receptive fields is presumably due to the heavy projections inferotemporal cortex receives from the regions of V4, V4A, and V5 onto which the foveal representation in V2 and V3 projects (Cowey, personal communication). The responsiveness to stimuli in the ipsilateral visual field presumably derives from the interhemispheric connections of V4, V4A, and V5 through the corpus callosum or possibly the interhemispheric connections of inferotemporal cortex itself.

The unexpected loss of discrete receptive field organization after the pulvinar lesions has interesting implications. It suggests that the receptive field boundaries of neurons in inferotemporal cortex may be determined, at least in part, by the pulvinar. This hypothesis is consistent with both the apparent absence of retinotopic organization in the areas of the circumstriate belt that project to inferotemporal cortex and with the presence of retinotopic organization in the pulvinar. The apparent dependence of the inferotemporal receptive field boundaries on the pulvinar suggests that in the behaving animal the pulvinar may modulate receptive field size as a function of attention or some other state of the animal (see Goldberg, and Wurtz, 1972).

In summary, the visual responsiveness and stimulus specificities of inferotemporal neurons are dependent on...
the input they receive from striate cortex by way of synapses in the circumstrial belt. The receptive field boundaries of inferotemporal neurons appear dependent on the projections they receive from the pulvinar.

Concluding comments

The behavioral effects of inferotemporal lesions indicate that inferotemporal cortex is involved in visual pattern recognition. Broadly viewed, pattern recognition includes (a) detection of stimulus features, (b) their synthesis across time and space and integration with eye and body movements, and finally, (c) the storage and retrieval of visual information. In the introductory portion of this chapter we speculated that the anatomical connections of inferotemporal cortex indicated that it might be involved in all three aspects of pattern recognition. How do our experimental results bear on these speculations?

The projections inferotemporal cortex receives from the circumstrial belt indicate that inferotemporal cortex might be a further stage in the hierarchy of feature detection mechanisms described by Hubel and Wiesel in striate and circumstrial cortex of the cat and monkey. They have proposed that the geniculostriate system consists of a series of converging and diverging connections such that at each successive tier of processing mechanisms, single neurons respond to increasingly specific visual stimuli falling on an increasingly wider area of the retina (Hubel and Wiesel, 1962, 1968). This hierarchy continues into the circumstrial belt (or prestriate cortex) where cells with still more specific trigger features and larger receptive fields are found (Hubel and Wiesel, 1965, 1970). Our finding that the visual responsiveness of inferotemporal neurons depends on striate cortex certainly indicates that inferotemporal cortex further processes visual information received from the geniculostriate system. Some of the neurons in inferotemporal cortex that had properties that continue the trends seen in ascending the geniculo-striate-circumstrial system: They had larger receptive fields and more specific trigger features than neurons in striate and circumstrial cortex. Thus, the properties of at least some inferotemporal neurons support the idea that inferotemporal cortex is a further stage in the hierarchy of stimulus feature detection that begins in the geniculo-striate system.

However, the majority of inferotemporal neurons, although they had large receptive fields, appeared less sensitive to such stimulus parameters as length, width,
and orientation than the cells in striate and circumstriate cortex described by Hubel and Wiesel (see, however, Poggio, 1972). This apparent lack of specificity may have been because these cells had complex and specific trigger features that we never found. The existence of cells in our sample with very complex trigger features is consistent with this possibility. On the other hand, these cells could have other functions than to continue the hierarchy of feature detectors begun in the geniculostriate system. They might be involved in some fundamentally different type of stimulus analysis mechanism, such as one involving Fourier-like analysis (see Pollen et al., 1971) or one involving ensembles of cells. Or, they might be concerned with the other two facets of pattern recognition, integration with head and eye movement, and storage and retrieval.

In the introduction, we proposed that the tectopulvinar input to inferotemporal cortex implied that inferotemporal cortex might integrate or "where it is" functions of the tectum with the feature detection or "what it is" functions of the geniculostriate system. The finding that receptive field boundaries disappear after pulvinar lesions lends some support to this possibility. We also speculated that inferotemporal cortex might be involved in gnostic and mnemonic functions. The extreme specificity of a few inferotemporal units, perhaps the result of experience, is consistent with this possibility. However, the present experiments are not really adequate tests of these hypotheses. The speculation that the activity of inferotemporal neurons depends on more than the retinal stimulus—that it also depends on the orientation of the animal toward the stimulus and on the meaning of the stimulus for the animal must be directly tested in behaving and thinking monkeys not in paralyzed anesthetized ones.

**Summary**

In primates inferotemporal cortex is a "higher" visual area. Its removal produces a severe deficit in visual learning while leaving basic visual functions and learning in other modalities unaffected.

We have studied the visual properties of single neurons in inferotemporal cortex. They had receptive fields that always included the fovea and were relatively large. Many fields extended into both visual half-fields; some were confined to the contralateral or ipsilateral half-field. Most inferotemporal neurons were sensitive to several parameters of the stimulus such as contrast, wavelength, size, shape, orientation, and direction of movement. Some had highly complex stimulus requirements.

Inferotemporal cortex receives a corticocortical input from striate cortex by way of synapses in the circumsstriate belt and a subcortical input from the pulvinar. We have shown that the visual responsiveness and trigger features of inferotemporal neurons depend on the corticocortical input from striate cortex whereas the receptive field boundaries appear to depend on the subcortical input.

The results suggest that at least some inferotemporal neurons form a further stage in the hierarchy of pattern recognition mechanisms that begin in the geniculostriate system. Other possible functions for inferotemporal cortex were proposed.

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**References**


