Visual Properties of Neurons in Inferotemporal Cortex of the Macaque

C. G. GROSS, C. E. ROCHA-MIRANDA, AND D. B. BENDER

Department of Psychology, Princeton University, Princeton, New Jersey 08540

IN THE LAST DECADE, considerable progress has been made in understanding the physiology of one of the most fundamental aspects of human experience: perception of the visual world. It is now clear that the retina and visual pathways do not simply transmit a mosaic of light and dark to some central sensorium. Rather, even at the retinal level, specific features of visual stimuli are detected and their presence communicated to the next level. In cats and monkeys, the geniculostriate visual system consists of a series of converging and diverging connections such that at each successive tier of processing mechanism, single neurons respond to increasingly more specific visual stimuli falling on an increasingly wider area of the retina (19–21).

How far does this analytical-synthetic process continue whereby individual cells have more and more specific trigger features? Are there regions of the brain beyond striate and prestriate[1] cortex where this processing of visual information is carried further? If so, how far and in what way? Are there cells that are concerned with the storage of visual information as well as its analysis?

There are several lines of evidence suggesting that a possible site for further processing of visual information and perhaps even for storage of such information might, in the monkey, be inferotemporal cortex—the cortex on the inferior convexity of the temporal lobe. First, this area receives afferents from prestriate cortex which itself processes visual information received from striate cortex (26). Second, bilateral removal of inferotemporal cortex has specific effects on visually guided behavior. After inferotemporal lesions, visual discrimination learning is severely impaired but discrimination of auditory, tactile, gustatory, and olfactory stimuli remains unaffected (see review by Gross, ref 15). In spite of this visual learning deficit, other more "basic" visual functions appear intact: inferotemporal lesions do not produce visual field scotomata nor do they affect visual acuity, critical flicker frequency, the threshold for detection of a brief visual stimulus, or backward masking functions (see ref 15). Thus, the impairment appears to be one of some "higher" visual functions. Such a syndrome does not follow ablation of other cortical areas. In fact, large partial lesions of striate cortex itself, while producing scotomata and visual threshold changes, have relatively little effect on visual learning (6). Third, visual-evoked responses can be recorded from macroelectrodes in inferotemporal cortex and single neurons in inferotemporal cortex respond to visual but not to auditory stimuli (13, 16, 18, 37).

Although this evidence establishes inferotemporal cortex as a visual area, it indicates little about its specific roles in vision. In this paper we report the existence of visual receptive fields of inferotemporal neurons and describe some of their properties. In a subsequent paper we will discuss the afferent basis of these properties.

METHODS

Animal preparation and maintenance

Seventeen *Macaca mulatta* weighing between 2.5 and 10 kg were used. Two to four days before the start of recording, the base of the microdrive and two bolts for subsequent fixa-

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[1] In this paper the terms "prestriate cortex," "circumstriate belt" of Kuypers et al. (26), and "areas OA and OB" of von Bonin and Bailey (2) are used synonymously.

tion of the head were implanted under thiopental sodium or pentobarbital sodium anesthesia. The microdrive and the bolts and their methods of implantation were essentially similar to those described by Evarts (10, 11). After excision of the temporal muscle, a ⅝ inch hole was trephined in the temporal bone and the base of the microdrive mounted over the opening. The dura was left intact and the microdrive base was filled with an antibiotic mixture (bacitracin 200 U/ml, polymixin B sulfate 0.1%, neomycin sulfate 0.5%) and capped. In some animals, microdrive bases were implanted bilaterally. The bolts were implanted in the frontal bone and emerged through stab wounds in the skin. After the animal's galea, muscle, and skin incisions were sutured, nitrofurazone ointment was applied topically and benzathine penicillin G given intramuscularly.

On the first recording day, the monkey was anesthetized intravenously with sodium thiamylal for the duration of a tracheotomy and vein cannulation. It was then immobilized with a continuous infusion of gallamine triethiodide in a solution of 5% dextrose in lactated Ringer solution, artificially respired, and anesthetized with a mixture of 30% oxygen and 70% nitrous oxide. (Succinylcholine chloride was used as the immobilizing agent in a few early experiments.) The stroke volume and rate of the respirator were adjusted to maintain the CO_2 content of the expired air at 3–4% as measured with a Beckman CO_2 analyzer. The animal's temperature was maintained between 37 and 39 C with the aid of a thermostatically controlled heating pad and heart rate continually monitored. The early experiments continued for 3 days and the later ones 4–5 days. The method of holding the animal's head by the implanted bolts provided an unobstructed visual field and facilitated adjustment of the position of the eyes.

The pupils were dilated with 0.25% scopolamine hydrochloride and the eyelids retracted. The eyes were fitted with contact lenses chosen with a slit retinoscope to bring the eyes in focus at a plane 57 cm away to the nearest 0.5 diopter. For each eye, the fovea, the center of the blind spot, and two venous junctions near the blind spot were projected onto the tangent screen with a reversible ophthalmoscope. A line passing through the projection of the center of the blind spot and fovea was taken as the horizontal meridian and an orthogonal line passing through the projection of the fovea was taken as the vertical meridian although, in fact, the precise center of the blind spot usually lies very slightly below the horizontal meridian. The combined errors in locating and projecting these landmarks were 0.5–1.0°. With the immobilizing techniques described above, the position of the eyes sometimes drifted 1–2° over several hours and no attempt was made to reduce this drift by additional techniques. Rather, the position of the eyes was replotted immediately before and after each detailed field plotting. Eye shields were arranged to allow monocular stimulation. Each night the contact lenses were removed, the eyes washed with saline and chlortetracycline hydrochloride ophthalmic solution, and then closed for several hours.

Recording techniques

Glass-coated platinum-iridium microelectrodes similar to those described by Wolbarsht et al. (38) were used. Their tips were cone shaped with about 20 μ from the tip exposed and with a diameter of about 4 μ at a point 22.5 μ from the tip. Their capacitance in agar-saline was between 15 and 30 pf according to a Tektronix LC meter. They were advanced with a microdrive similar to that described by Evarts (10, 11). The signals from the electrode were led to a cathode follower mounted on or near the microdrive, and then to a preamplifier, displayed on an oscilloscope, put through an audio amplifier into a speaker, and recorded on magnetic tape. Only signals that clearly came from an isolated single neuron as determined by constant amplitude and waveform were studied. In addition, EEG was recorded from needle electrodes in the scalp over the occipital lobe, amplified, displayed on an oscilloscope, and recorded on magnetic tape.

Visual stimuli

To prevent adventitious stimulation with stray light, the animal was placed in a tent of black cloth. A 70 cm x 70 cm translucent Polacoat tangent screen was mounted in the tent wall perpendicular to the visual axis, 57 cm from the eyes and adjusted so that the projection of the foveae fell near the center of the screen.

Two types of visual stimuli were used, "light" and "dark." The light stimuli were projected onto the rear of the tangent screen by an optical apparatus consisting of tungsten filament light source, lenses, dove prisms, slides, neutral density filters, and often Wratten color filters, all mounted on a movable optical bench. One dove prism was mounted on a galvanometer coil so that stimuli could be moved across the tangent screen either automatically by a waveform generator, or manually by adjusting a potentiometer. The location of the stimulus on the screen was indicated by photocells mounted

on the screen and by a voltage output from the galvanometer. Both the state of the photocells and the galvanometer voltage were recorded on magnetic tape along with the bioelectric signals.

Although a great variety of light stimuli were used, most cells were tested with certain relatively "standard stimuli." The standard background luminance of the tangent screen was 1.5 mL. The standard light slit was 1° wide with a luminance of 1.5 log units greater than standard background. Three color filters were occasionally used: red (Wratten filter 29), green (Wratten filter 40), and blue (Wratten filter 47). When these were used, the background luminance was usually reduced to .1 mL and the luminance of the red light was 1.7 log units greater than this background, the luminance of the green light 1.9 units greater and the luminance of the blue light .6 log units greater. All luminance measures were made with a Pritchard spectra photometer. The standard rate of the automatic sweep was between 5 and 7°/sec.

The standard dark stimuli were cardboard cutouts moved manually on the back of the tangent screen with standard background illumination. Their luminance was 2.2 log units below the background.

Receptive-field plotting

The method of plotting receptive fields varied with the response characteristics of the neuron. Thus if the neuron responded equally well to horizontal and vertical slits 1° wide, its field boundaries were determined by moving the slits both horizontally and then vertically across the tangent screen. However, if it responded only to a vertical slit moving orthogonally to its long axis, the lateral boundaries of the field were determined by horzontal movement of the slit, and the upper and lower boundaries by varying the length and vertical position of the slit as it moved horizontally. The stimuli were moved and the receptive fields detected with two methods. In the first, the presentation and movement of the stimulus were controlled by hand and the field borders were detected by listening to the discharges of the isolated unit and marking the boundaries on the screen. In the second, the stimulus was automatically moved across the screen synchronously with the sweep of a Mnemotron Computer of Average Transients (CAT), thus providing a plot of the frequency of firing of the isolated unit as a function of the location of the stimulus. Usually such histograms were generated by 10 sweeps of the stimulus in each direction. For units responsive to standard light stimuli, fields were usually plotted with both methods, which invariably yielded similar receptive fields. With both methods the receptive fields corresponded to the "minimal receptive fields" of Barlow et al. (1). Cells responsive to dark stimuli or nonstandard light stimuli were plotted only with the first method (hand plotting). Plotting with slits of light or edges usually yielded rectangular receptive fields, whereas with other stimuli, the shape of the fields were often not rectangular. However, if the unit responded to both types of stimuli, then the receptive field plotted with each had a similar area and similar location of its geometric center. The histograms presented in this paper were generated by reanalysis of tape recordings of the original raw data with a Digital Equipment Corp. PDP-12 computer with close monitoring of both the waveform of the isolated unit to insure absence of contamination by other signals and of the state of the EEG.

As this study progressed, we learned more and more about the optimal conditions necessary to elicit responses from inferotemporal units and altered our methods of plotting receptive fields accordingly. Among the procedures introduced after several experiments were: *1*) use of dark stimuli; *2*) use of colored stimuli; *3*) use of interstimulus intervals up to a few minutes; *4*) use of irregular and highly complex stimuli; and *5*) most importantly, close monitoring of the EEG and its maintenance in a low-voltage, high-frequency state by presenting somesthetic, acoustic, and olfactory stimuli. Such "arousing" stimuli were presented in the intervals between visual stimulation. Indicative of the importance of these factors was that in the earlier experiments many receptive fields could only be plotted by using the CAT, whereas later, almost all fields could be plotted by moving the stimuli by hand and listening to the loudspeaker.

Histological methods

At the conclusion of each experiment, the monkey was perfused through the aorta with saline followed by 10% formalin. A week later the brain was cut in the coronal stereotaxic plane, cast in dental impression compound, and cut in 25-μ frozen sections which were stained with cresyl violet. The approximate site of entry of each electrode was marked on the cast and its path was reconstructured from the serial sections. The cortex through which the electrode passed was classified according to the cytoarchitectonic criteria of von Bonin and Bailey (2). In addition, the site of entry of each pass was marked on a standard brain drawing (Fig. 1).

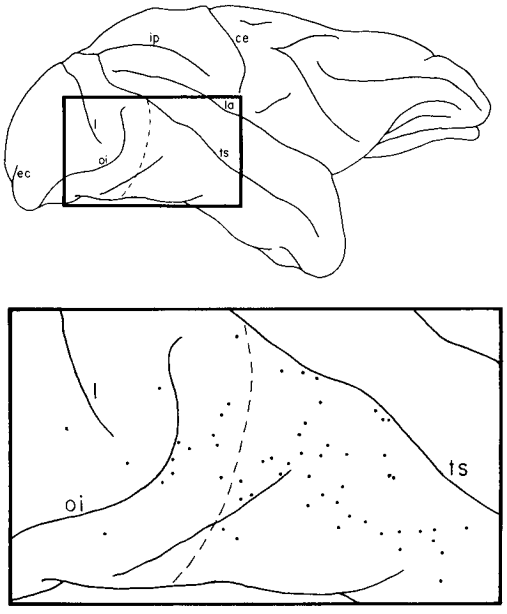

FIG. 1. *Upper:* lateral view of cerebral hemisphere of *Macaca mulatta* showing site of lower drawing. *Lower:* site of entry of electrode passes. Passes made in the left hemisphere are shown in the corresponding sites of the right hemisphere. Passes to the right of the dashed line were in cytoarchitectonic area TE and those to the left were in area OA or in cortex transitional between area OA and area TE (see text). The dashed line represents the typical posterior border of cortex clearly distinguishable as area TE. ce = central sulcus, ec = external calcarine sulcus, ip = intraparietal sulcus, l = lunate sulcus, la = lateral fissure, oi = inferior occipital sulcus, ts = superior temporal sulcus.

RESULTS

Two hundred and sixty-three neurons in the cortex of the inferior convexity of the temporal lobe were studied in sufficient detail to make some statement about their properties. They were divided into two groups, group OA and group TE, on the basis of the cytoarchitectonic criteria of von Bonin and Bailey (2). (They give several distinguishing characteristics of areas OA and TE. We found those pertaining to layers iii and v the most reliable.) Group OA neurons (N = 58) were located in cortex that was either OA cortex or cortex transitional between OA and TE and located within 2 mm of OA cortex. As shown in Fig. 1, these passes were located near the ascending portion of the inferior occipital sulcus, and thus in the most anterior portion of area OA and the circumstriate belt.[1] Group TE neurons (N = 205) were all located in the posterior and middle portions of area TE. The site of entry of the electrode passes on which OA and TE units were recorded is shown in Fig. 1. A coronal section through one pass is shown in Fig. 2. For purposes of exposition, neurons in both groups will be referred to as "inferotemporal neurons," although this term, strictly speaking, should only refer to the TE units.

With the standard background illumination, all neurons encountered were spontaneously active with almost all discharge rates falling in the range 1–30/sec. The activity of 86% of the OA units and 82% of the TE units was altered by visual stimulation.[2] Most of these units responded exclusively by increasing their rate of discharge (72% of TE units, 62% of OA units). For other units only decreased firing to visual stimuli could be demonstrated (20% of TE, 12% of OA units). The remaining ones showed either increased or decreased firing over the spontaneous level depending on the retinal locus, direction of movement, or other stimulus parameters. Significantly more OA units (26%) than TE units (8%) fell in this class (χ^2 test, $P < .005$).

No neurons were found that responded to auditory or somesthetic stimuli. A few passes were made through superior temporal cortex (area TA). Units recorded on these passes responded only to auditory stimuli and not to visual, confirming our earlier observations under different anesthetic conditions (18).

Receptive fields

SIZE. We determined the receptive-field sizes of 116 neurons. The areas of the largest fields were probably often underestimated since fields extending to a border of the tangent screen were taken to end at that border. If receptive fields were plotted for both eyes, the size of the receptive field of

[2] These percentages are probably inflated by the fact that the time required to demonstrate a response was often less than the time required to classify the cell as "unresponsive," and cells were occasionally left or lost before they had been studied sufficiently to be classed as unresponsive and were therefore excluded from our sample.

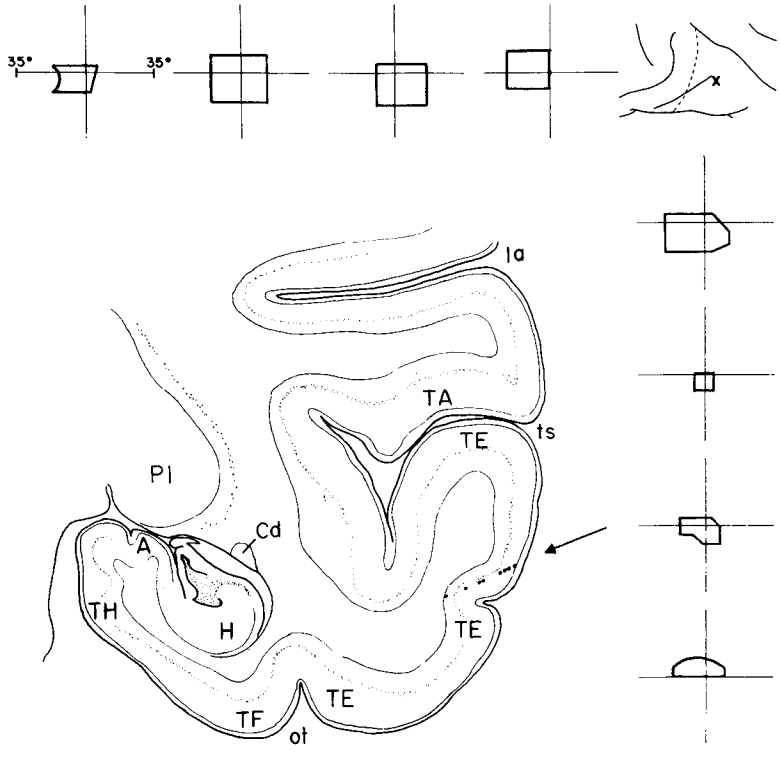

FIG. 2. Coronal section in plane of electrode pass (arrow) in inferotemporal cortex showing approximate location of eight representative cells recorded on the pass and the size and location of their receptive fields. The receptive fields recorded at increasing depth are shown clockwise starting from the top left. In these and all following receptive-field maps, 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. In the inset brain drawing, x marks the site of entry of the electrode pass. la = lateral fissure, ot = occipitotemporal sulcus, ts = superior temporal sulcus, cd = caudate nucleus, H = hippocampus, Pl = pulvinar; TA, TE, TF, TH, and A refer to cytoarchitectonic areas (2).

the dominant eye was used to estimate the size of the neuron's receptive field.

The receptive fields were surprisingly large; those of the TE units were usually larger than those of the OA units. The median area of the receptive fields of TE neurons (N = 86) was 409 deg^2 with first and third quartiles of 145 and 1,410 deg^2, while the median area of the OA fields (N = 30) was 69 deg^2 with the first and third quartiles of 14 and 140 deg^2. This difference in size was significant beyond the .0001 level according to a Mann-Whitney U test. Representative receptive fields are shown in Figs. 2, 4, 5, and 7.

The large size of many of the receptive fields, particularly in group TE, was unlikely to have been the result of some optical artifact, because with the same apparatus and procedures, and often in the same

animal, receptive fields of under a square degree were found for units in the circumstriate belt (areas OA, OB) and in striate cortex (area OC). Similarly, scattered light could not easily account for the large size of the fields since there was no difference in the size of the fields when contrast or background illumination was varied over a wide range.

LOCATION. Perhaps the most surprising finding was that, within the accuracy of measurement, the center of gaze or fovea fell within or on the border of the receptive field of every inferotemporal neuron studied.

Unlike those in the geniculostriate system, many receptive fields extended well across the midline into the half-field ipsilateral to the electrode, and some were even confined to the ipsilateral half-field. Lateral borders were determined for 33 OA cells and 95 TE cells. More of the TE cells (56%) than OA cells (30%) had receptive fields which were clearly bilateral (i.e., extended more than 3° into both visual half-fields), although this difference failed to reach significance according to a χ^2 test. Of the essentially unilateral receptive fields (i.e., those extending more than 3° into one half-field and less than 3° into the other half-field) ipsilateral fields were more common in the OA Group (57%) than in the TE Group (20%) according to a χ^2 test ($P < .05$).

The geometric centers of the receptive fields are shown in Fig. 3. Note that for both groups, the centers of the "bilateral" receptive fields were predominantly (79%) located in the contralateral half-field (binomial test, $P < .001$).

About half of the cells responded more strongly when stimulated in one part of their receptive field. This more responsive area always included the fovea and extended, within the receptive field, 3–20° from the fovea. This phenomenon of a stronger response over the fovea is illustrated in Figs. 4 and 5. Among the neurons with bilateral fields, stimulation of the contralateral portion often elicited a stronger response than stimulation of the ipsilateral portion, whereas the converse was very rarely found.

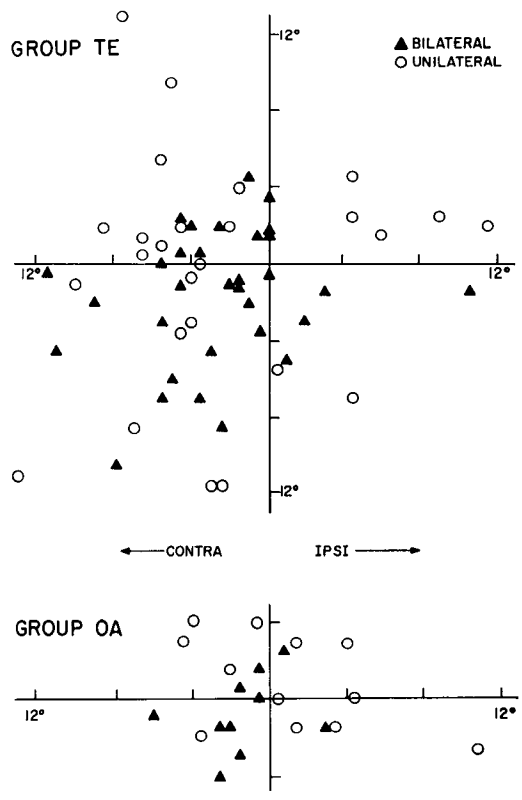

FIG. 3. Geometric centers of receptive fields. Axes represent the horizontal and vertical meridia. The scale is in degrees of visual angle. ipsi is the half-field ipsilateral to the electrode and contra the contralateral half-field. Cells designated as bilateral extended more than 3° into both half-fields and those designated as unilateral extended more than 3° into one half-field and 3° or less into the other half-field. This sample excluded cells whose receptive fields extended to at least one border of the 70° x 70° tangent screen and cells whose receptive fields extended 3° or less into either half-field. (The latter fields, since they included the center of gaze, like all other fields, necessarily had geometric centers within 1.5° from this point.)

Effects of stimulus parameters

MOVEMENT. Almost all the units responded more vigorously to a moving stimulus than to a stationary one. Although rate of movement was not systematically varied for a large number of units, most neurons did seem to respond to the standard rate of 5–7°/sec better than to much higher or lower rates of movement.

LIGHT VERSUS DARK. Of the 226 neurons tested with light stimuli, 71% responded to light stimuli, and of the 186 neurons tested with dark stimuli, 69% responded to dark

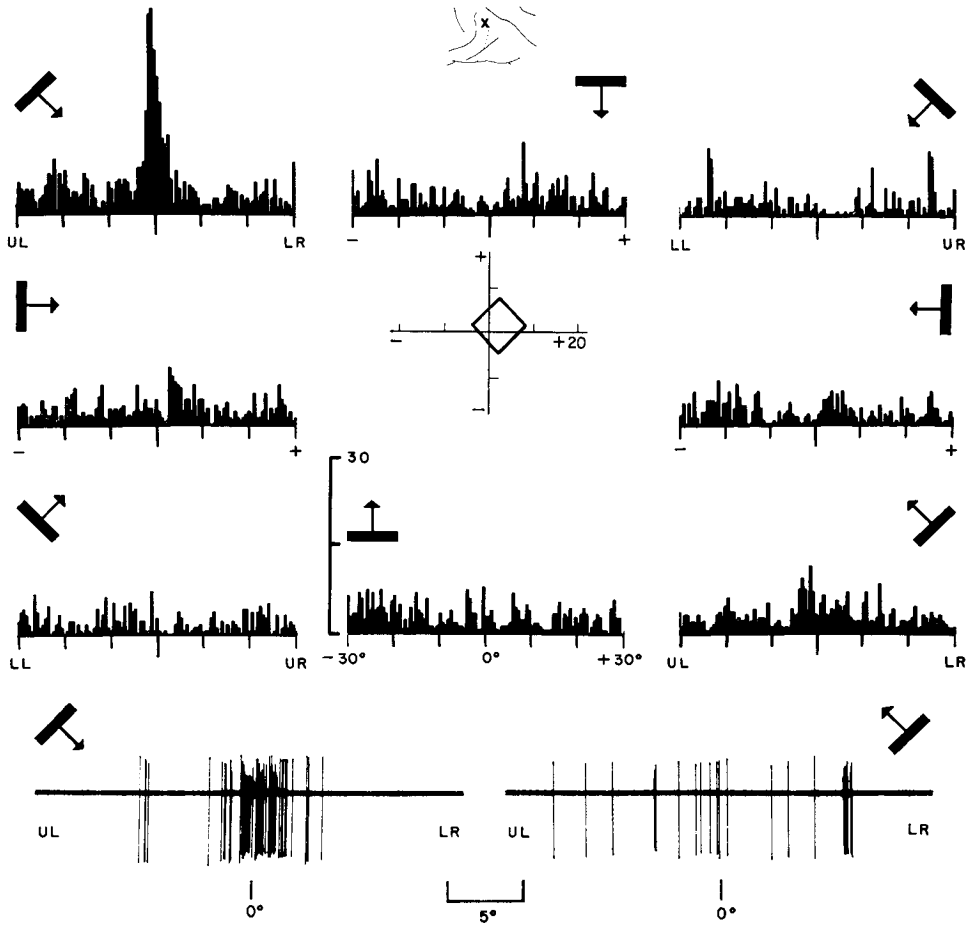

FIG. 4. Receptive field and responses of a group OA neuron which showed unidirectional sensitivity. Histograms indicate frequency of firing of the unit as a function of retinal locus of a 1° x 70° red slit moving at 5°/sec in the direction indicated above each histogram. Each histogram was generated by 10 sweeps of the stimulus. For the eight histograms, the vertical scale indicates number of neuron discharges and the horizontal scale, degrees of visual angle; the middle of each horizontal scale (0°) represents the center of gaze. The receptive field of this unit is shown in the center of the array of histograms. Plus (+) in all parts of the figure inidcates upper or right of the visual field; minus (−) indicates lower or left; UL, upper left; LR, lower right; LL, lower left; UR, upper right. The lower part of the figure shows the discharges of an isolated unit to a single sweep of the stimulus in the indicated direction on an expanded time scale. Histograms and trace in which the arrow is shown on the left were generated from left to right, whereas the converse was true where the arrow is shown on the right. The site of the pass on which this was recorded is shown in the top center of the figure. See also legends to Figs. 1 and 2.

stimuli. Of the 151 neurons studied with both dark and light stimuli, 48% responded to both types of stimulation. These proportions were similar for the OA and TE groups. Whether a neuron responded to dark, light, or both types of stimuli did not appear correlated with its other properties.

SIZE AND SHAPE OF STIMULI. Our set of frequently used stimuli was impoverished relative to the possible set of arbitrary stimuli we could have used or even to a set of stimuli "relevant" to a monkey. Since, in our earlier preparations, circles and rectangles of light were usually much less effective stimuli than light slits, we soon abandoned systematic use of the former stimuli. A few TE neurons, however, did seem to prefer a 3° diameter circle or a 5° x 5° square to the standard 1° slit. 10° x

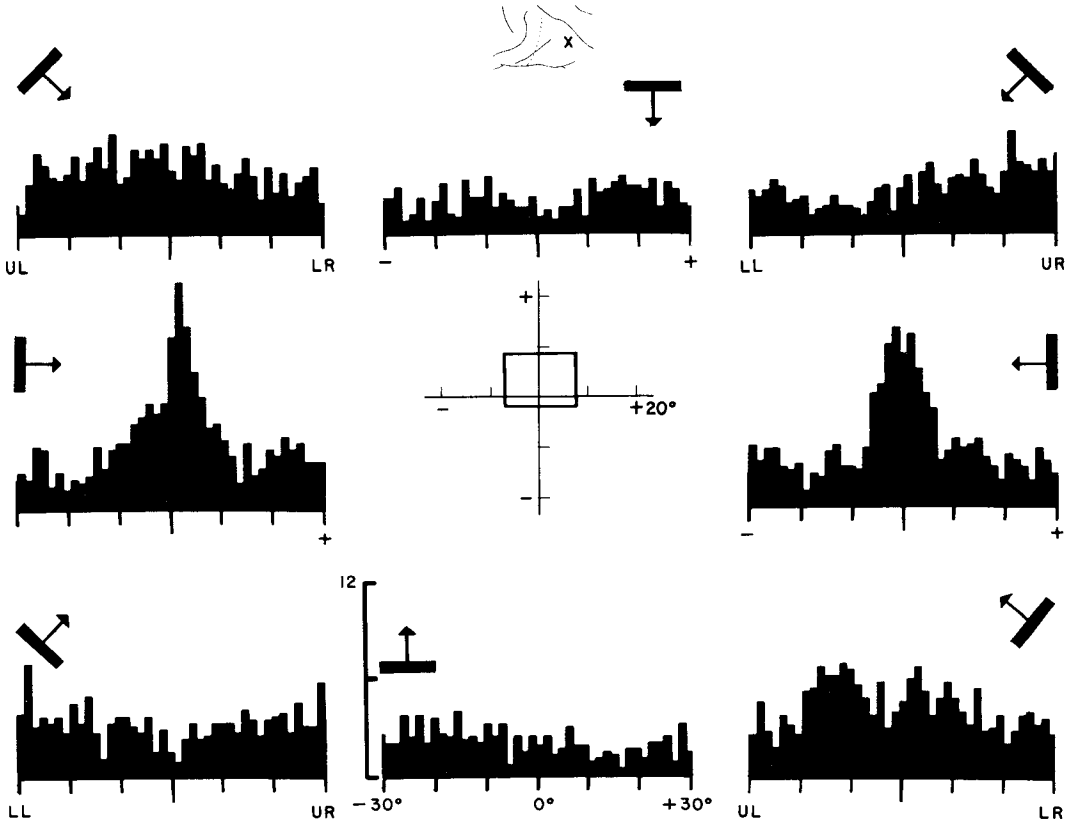

FIG. 5. Receptive field and responses of a group TE neuron which showed bidirectional sensitivity. The stimulus was a white slit 1° x 70° moving at 5°/sec. Each histogram is based on seven sweeps of the stimulus. See also legends to Figs. 1, 2, and 4. Responses of this neuron to single sweeps of the stimulus are shown in Fig. 8.

5° and 5° x 5° checkerboards were good stimuli for several units, but these stimuli were later abandoned because of the difficulty in determining exact field boundaries with them. For most neurons, a light slit 1.0° wide yielded stronger responses than either a much wider or narrower one. Surprisingly, the length of the slit did not appear critical for many neurons in either group. For at least three TE units, complex colored patterns (e.g., photographs of faces, trees) were more effective than the standard stimuli, but the crucial features of these stimuli were never determined. Of the neurons tested to a diffuse light flash, about one-third responded, usually in a very weak fashion.

Our dark stimuli were also less than ideal, both in their poverty and in their lack of correspondence to the standard light stimuli. However, the greater ease of producing dark stimuli (by picking up objects at hand or making paper cutouts) did yield some interesting observations. The most common dark stimuli used were a variety of rectangles or slits with widths of .25–30° and lengths of 1–70°, and the shadow of a human or monkey hand. The use of the latter stimuli was begun one day when, having failed to drive a unit with any light stimulus, we waved a hand at the stimulus screen and elicited a very vigorous response from the previously unresponsive neuron. We then spent the next 12 hr testing various paper cutouts in an attempt to find the trigger feature for this unit. When the entire set of stimuli used were ranked according to the strength of the response that they produced, we could not find a simple physical dimension that correlated with this rank order. However, the rank order of adequate stimuli did correlate with simi-

larity (for us) to the shadow of a monkey hand. The relative adequacy of a few of these stimuli is shown in Fig. 6. Curiously, fingers pointing downward elicited very little response as compared to fingers pointing upward or laterally, the usual orientations in which the animal would see its own hand.

Of the 128 neurons that responded to dark stimuli, about 50 fired best to one of the rectangular stimuli, the smaller ones usually being better. For the remaining neurons, particular complex dark stimuli were the best stimuli we could find.

Several neurons fired much more strongly to three-dimensional objects placed in the plane of the tangent screen than to any stimulus projected onto the screen, including two-dimensional representations of that object. This rather surprising phenomenon was observed with monocular as well as binocular stimulation.

In summary, although our explorations of stimulus size and shape were limited and nonsystematic, certain conclusions can be drawn with some certainty. First, approximately 1° wide light slits were usually more powerful stimuli than light circles, rectangles, wider slits, or diffuse light. Second, there were units whose response depended on the length and width of the light slit. Third, there were units that would respond vigorously to specific and complex dark shapes but not to dark slits or to dark rectangles of similar overall dimensions. (More of the TE units than the OA units responded to unusual stimuli, but this may simply have reflected the greater ease of driving the OA units with the standard stimuli, and the consequent lesser tendency to test them with irregular stimuli.) Fourth, few units responded in identical fashion with one another to a range of stimuli (except for several clusters of two to five units recorded on the same pass at similar depths). Rather, although responses to certain stimuli were common, most units seemed to have their own unique preference spectra. Finally, with the exception of one cell, the optimum stimulus for a cell was optimum throughout the receptive field, even for cells with large bilateral fields.

ORIENTATION AND DIRECTION OF MOVEMENT. Virtually all neurons in both group OA and group TE responded best or only to moving stimuli. Furthermore, if the neuron was sensitive to the orientation of the stimulus, the optimal orientation was almost always orthogonal to the optimal direction of movement. Therefore it was usually not meaningful to distinguish sensitivity to orientation of a stimulus from sensitivity to its direction of movement. Responses to a stimulus moving orthogonally to its long axis in four directions 90° apart were systematically compared for 24 OA units and 64 TE units. If a unit fired differentially to two of these directions of movement it was defined as being "direction sensitive" without implying anything about the underlying mechanism. Some direction-sensitive neurons respond equally well to movements 180° apart (preferred directions) but poorly or not at all to orthogonal directions (null directions). These are termed "bidirection sensitive" units. Other direction-sensitive neurons responded best to one direction of movement and had null directions 90° to the preferred direction. These are termed "unidirection sensitive" neurons.

A far greater proportion of OA units (83%) than of TE units (48%) were direction sensitive (χ^2 test, $P < 0.005$). Of the direction-sensitive neurons most of the ones in group TE (85%) but only half the ones in group OA were bidirection sensitive (difference significant at the 0.01 level, χ^2 test). Responses of a typical unidirection-sensitive OA unit are shown in Fig. 4 and of a typi-

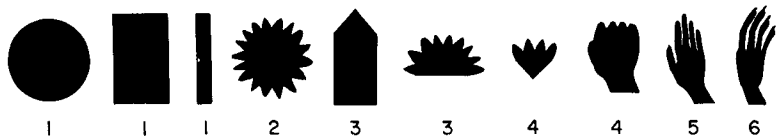

FIG. 6. Examples of shapes used to stimulate a group TE unit apparently having very complex trigger features. The stimuli are arranged from left to right in order of increasing ability to drive the neuron from none (1) or little (2 and 3) to maximum (6).

cal bidirection-sensitive TE unit in Figs. 5 and 8. The directional sensitivity was the same everywhere in the receptive field, with the exception of one cell (ref 16, Fig. 3). For most of the cells tested, directional sensitivity was independent of contrast.

There were a few units that were exceptions to the generalization that the best orientation of a stimulus was orthogonal to its best direction of movement. These included three units that preferred handlike dark stimuli (for which the orientation of the fingers independent of the direction of movement was critical), two that preferred movement of a slit parallel to its long axis, and one that fired best to a moving vertical slit independent of the direction of movement.

We observed only two units for which the preferred direction of movement was different between the two eyes. The receptive-field location and the response properties were similar, as usual, in the two eyes, except that the preferred direction of movement within the receptive field of each eye was mirror symmetric along the vertical meridian (ref 16, Fig. 3).

COLOR. We had not intended to test sensitivity to wavelength. However in an early experiment after the standard dark and light stimuli failed to drive a unit, we tried some colored slides, and elicited strong responses. Subsequent study of this unit revealed that red or orange stimuli were required to drive it. Thereafter, in searching for an adequate stimulus to plot receptive fields we often projected red, green, or blue slits.

Although colored stimuli appeared to be particularly effective in driving many units, we did not plot their spectral sensitivity. However, in 19 of 52 units for which we compared the response to red, green, blue, and white stimuli, the magnitude of the response was not correlated with luminance of the stimuli. Most of these would respond vigorously to a red pattern (luminance 5 mL), but not at all to the same pattern when it was green (luminance 8 mL) or blue (luminance .4 mL). Neither would they respond when the pattern was white even though its luminance was varied over a range of 2.6 log units (.1–40 mL). Only two cells showed such a preference for green light and one did so for blue.

Four of the apparently color-sensitive cells (of 21 tested) were in group OA and 15 (of 31 tested) were in group TE, but no inferences about the incidence of color preferences in the two groups can be made since most of the units studied in any detail were units that were very difficult to drive with white light.

INTERSTIMULUS INTERVAL. Most of the neurons studied showed a decline in response when repeatedly stimulated at less than 5-sec intervals. Response strength could be maintained by increasing this interval. Units requiring more than 15 sec between stimulation for optimum response were more common in the TE group.

The responsiveness of a few of the TE units would decline in the course of a single sweep of an adequate stimulus across the receptive field at the standard (5–7°/sec) rate. Such a unit would fire briskly as a bar sweeping across the tangent screen entered the receptive field, but would show little response by the time it reached the opposite border (see Fig. 7). However, if introduced after several seconds of no stimulation, the bar would elicit an equally strong response any place within the receptive field.

EYE DOMINANCE. For 63 neurons, the relative effectiveness of stimulating the two eyes was determined. For both groups, one-quarter of the units responded more strongly to stimulation of the ipsilateral eye, one-quarter to stimulation of the contralateral eye, and half showed no clear difference between the eyes. The existence and type of eye dominance was not found to be related to the site of the unit or any other response characteristic. If responses could be elicited from both eyes, the receptive field center was approximately the same for both, as were the response properties, with the exception of the two units described above that had opposite directional sensitivity for the two eyes.

Effect of EEG state and barbiturate administration

After several experiments it was observed that, for almost all neurons, variations in the EEG were correlated with variations in

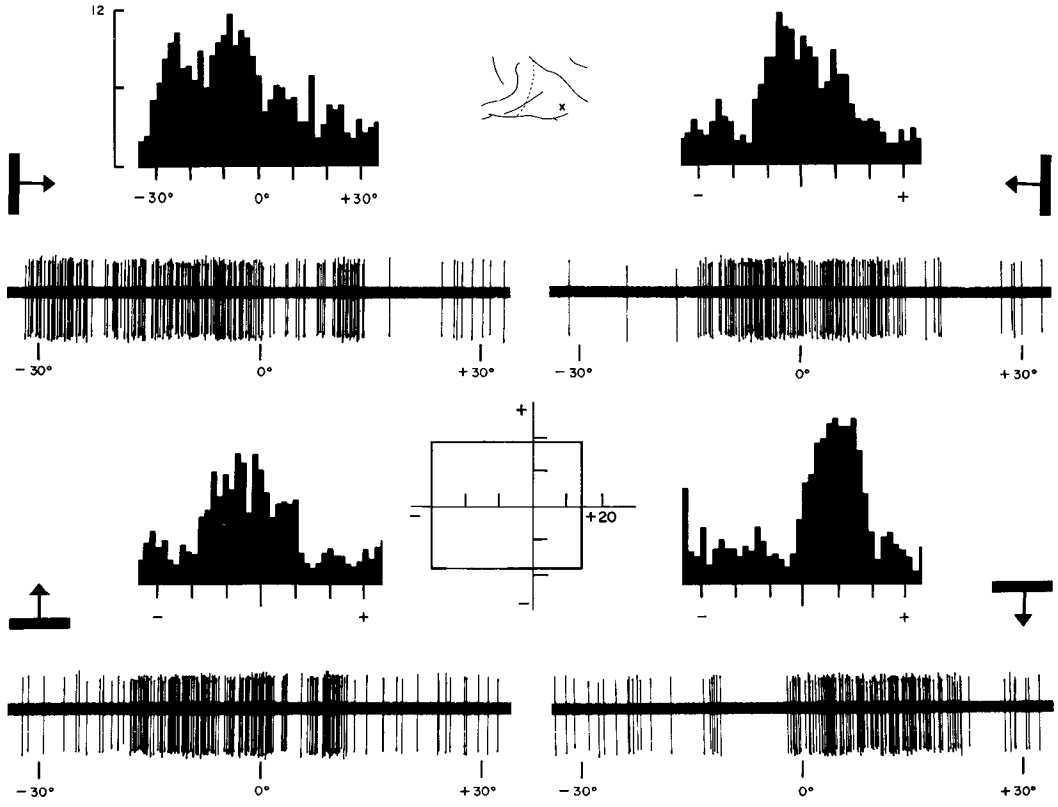

FIG. 7. Receptive field and responses of a group TE neuron which did not respond differentially to the orientation or direction of movement of a 1° x 70° white slit. Each histogram was generated by 10 sweeps of the stimulus moving in the indicated direction at 6.7°/sec. Note that the response is vigorous when the slit enters the receptive field but declines before the slit reaches the opposite border. See also legends to Figs. 1, 2, and 4.

the strength of a neuron's response. Neurons would respond vigorously during periods of low voltage, fast and asynchronous EEG (called hereafter "fast" EEG), but show little or no response during periods of relatively high voltage, slow and synchronous EEG (called hereafter "slow" EEG). This is illustrated in Fig. 8. In some units the pattern of spontaneous activity was different in states of fast or slow EEG, but in

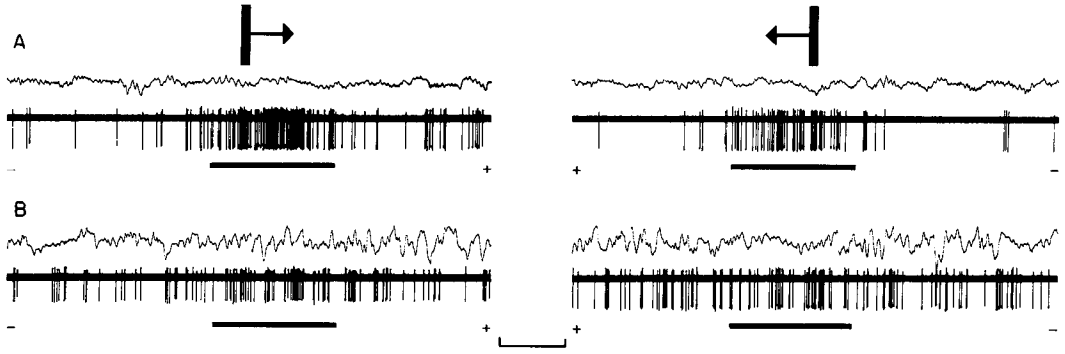

FIG. 8. Responses of a group TE neuron under two EEG conditions, *A*, fast, and *B*, slow (see text), to movement of a 1° x 70° white slit in the indicated direction at 5°/sec. The horizontal bars indicate the receptive-field location. This is the same neuron whose receptive field and histograms are shown in Fig. 5. The marker indicates 3 sec or 15°

others only changes in evoked activity were associated with changes in EEG.

Novel acoustic, somesthetic, and olfactory stimulation would return an animal in a state of slow EEG to its previous state of fast EEG, and simultaneously restore the unit's previous responsiveness. None of these novel stimuli would alter the unit's activity if the EEG was already fast. After these earlier observations were made, EEG was closely monitored during study of a neuron. When the EEG became slow it was returned to its previous fast state by acoustic, somesthetic, or olfactory stimulation before study of the unit continued. Novel somesthetic or auditory stimuli are also often required for full visual responsiveness of area 17 and area 18 neurons in the cat anesthetized with nitrous oxide and oxygen (J. D. Pettigrew, personal communication).

Intravenous injection of sodium thiamylal would totally eliminate first the responsivity of a unit to visual stimuli and then the ability to transform slow EEG into fast by peripheral stimulation. In time, the two phenomena would return in the opposite order.

DISCUSSION

Characteristics of inferotemporal neurons

COMPARISONS WITH OTHER VISUAL NEURONS. The most striking finding of this study was the relatively large receptive fields that invariably included the fovea. Such receptive fields do not appear to be characteristic of neurons in other brain structures. Another unusual finding was the large receptive fields that extended well into both visual hemifields. Cells with similar receptive fields have been found in the pulvinar (14) and anterior middle suprasylvian cortex (AMSS) of the cat (9). Apparently unique were the receptive fields confined to the ipsilateral half-field and extending more than 10° from the vertical meridian.

Two sets of inferotemporal neurons had properties that appeared relatively novel. One would respond only by decreased firing. That is, these cells would fire less when stimulated by particular stimuli (their "adequate" stimuli) but no stimuli could be found that would increase the rate of firing above the spontaneous level. Two similar cells have been previously reported in striate cortex of the cat (30). The other set of cells had opposite directional selectivity in the two eyes. However, both sets were small and similar neurons may turn up elsewhere in the brain. Similarly, although there were a number of inferotemporal neurons with strikingly specific and complex trigger features, the incidence of such cells in inferotemporal cortex and elsewhere is difficult to estimate.

Besides these unusual properties, inferotemporal neurons had many response properties similar to those of neurons in other visual structures. The preference for moving stimuli over stationary ones, preference for bars over spots of light, varying degree of eye dominance, and waning of response with repeated stimulation, typical characteristics of inferotemporal units, have also been reported for neurons in striate cortex, prestriate cortex, and the superior colliculus (e.g., 19–22, 30, 34). Most inferotemporal units resembled superior colliculus and AMSS units in the cat rather than visual cortex units in tolerating considerable variation in stimulus shape and direction of movement without altering their response (e.g., 9, 34). By contrast, other inferotemporal units were similar to visual cortex units and very different from colliculus units in their sensitivity to size, shape, and orientation of a stimulus (e.g., 19–21, 30).

The directional sensitivities of inferotemporal units were very heterogeneous. Many were not direction sensitive at all; while some had null directions 90° to the preferred direction, like units in visual cortex and some AMSS units in the cat; while others had null directions 180° to the preferred direction, like some colliculus and AMSS units in the cat (e.g., 9, 19–21, 30, 34).

The small number and widespread distribution of our passes and the acute angle at which almost all of them entered the brain made it impossible for us to determine if inferotemporal cortex has the columnar organization so characteristic of striate and prestriate cortex. We did observe a clustering of similar properties among neurons successively recorded on the same pass, but this could have reflected a laminar or

complex nesting organization almost as well as a columnar one.

COMPARISON OF GROUP TE AND GROUP OA NEURONS. The neurons we studied were in two different cytoarchitectonic areas according to the criteria of von Bonin and Bailey (2). The group OA neurons were in the part of area OA near the ascending portion of the inferior occipital sulcus, thus near the rostral border of circumstriate cortex. The group TE neurons were in the dorsal middle and posterior portions of area TE. Although OA and TE neurons shared many characteristics, the two groups differed in incidence of neurons with certain properties. OA units had smaller receptive fields and were more likely to show differential sensitivity to direction of movement of the stimulus. If direction sensitive, TE units but not OA units were much more likely to be bidirectional. Although both groups included neurons with bilateral, contralateral, and ipsilateral receptive fields, in the TE group, bilateral fields were more common and ipsilateral fields rarer.

Although the exact anterior border of the projection of striate cortex onto the circumstriate belt is unclear, it is likely that at most two passes (the most caudal) fell within it (cf. 7, 39; A. Cowey, unpublished data). Thus except for these two passes, the area we recorded from was connected to striate cortex by a minimum of two synapses. Cowey (unpublished observations) has shown that cells immediately anterior to the inferior occipital sulcus (i.e., in the area of our group OA cells) project diffusely throughout area TE. Therefore the properties of TE units might derive, at least in part, from converging inputs from OA neurons.

Functions of inferotemporal cortex

Bilateral ablation of inferotemporal cortex impairs visual learning while leaving both visuosensory function and learning ability in other modalities intact (see review by Gross, ref 15). Inferotemporal cortex receives direct projections both from the ipsilateral circumstriate belt and, by way of the splenium of the corpus callosum, from the contralateral circumstriate belt (26). In turn, each circumstriate belt receives a projection from both striate cortices (7, 39, 40). Interruption of this corticocortical occipitotemporal pathway impairs visual discrimination learning (5, 24, 28, 29). Therefore we (5, 15, 16, 32) and others (e.g., 4, 28) have hypothesized that this pathway carries visual information to inferotemporal cortex, where it is further processed. Such "processing" is presumed necessary for normal visual discrimination learning.

This hypothesis is directly supported by the present results in that they demonstrate that visual information does arrive at inferotemporal cortex and that this information is both specific and complex. Furthermore, the hypothesis that inferotemporal cortex further processes outputs of the circumstriate belt provides an explanation for two prominent properties of inferotemporal units, viz., the invariable inclusion of the fovea in the receptive fields and the existence of bilateral and ipsilateral receptive fields. The inclusion of the fovea would derive from the fact that inferotemporal cortex receives a heavy projection from the portion of prestriate cortex ("foveal prestriate cortex") onto which the foveal representation in striate cortex projects (7, 39). The ipsilateral and bilateral receptive fields would derive from the connections of the two circumstriate belts through the splenium of the corpus callosum (35) or the connections of the two inferotemporal cortices through the anterior commissure (12) or both connections.

Further support for the importance of the corticocortical input to inferotemporal cortex is the effects of its interruption on the visual properties of inferotemporal neurons. After total removal of one striate cortex, the receptive fields of inferotemporal neurons in both hemispheres are confined to the visual half-field contralateral to the intact striate cortex (unpublished observations). After section of the corpus callosum and anterior commissure, inferotemporal neurons have receptive fields confined to the visual half-field contralateral to the recording electrode (unpublished observations).

The next, and more difficult, question is how inferotemporal cortex processes the visual information it receives from the cir-

cumstriate belt. One hypothesis is that inferotemporal cortex is a further stage in the hierarchy of visual mechanisms shown by Hubel and Wiesel (19–21) to extend from the retina through the geniculostriate system to the circumstriate belt. The successive transformations of visual input that Hubel and Wiesel have proposed to occur in this system involve two chief principles. The first is increasing generalization across the retina: cells at higher levels can be driven by their adequate stimulus over wider regions of the retina. The second is increasing specificity of the adequate stimulus: orientation of a slit is not critical for ganglion or lateral geniculate cells but is critical for cortical cells; length of a slit is critical for hypercomplex but not simple or complex cortical cells. Hubel and Wiesel suggest that convergence of outputs from cells at a lower level underlie these transformations.

Virtually all inferotemporal neurons appear to continue the first trend: their receptive fields were much larger than those of complex and hypercomplex neurons with fields in comparable retinal areas. A few inferotemporal neurons appear to continue the second trend: they had more specific trigger features than have been reported for complex or hypercomplex cells. Many cells, however, appeared to be less sensitive to such stimulus parameters as length, width, and orientation than cells in striate and prestriate cortex. This apparent lack of specificity may have been because these cells had complex and specific trigger features that we never found. The existence of other cells in our sample with very complex trigger features supports this possibility. The observation that three-dimensional objects were far more adequate stimuli than two-dimensional patterns for some neurons also suggests that a wider range of stimuli might have revealed a greater stimulus specificity.

It is also possible that "stimulus adequacy" for some inferotemporal neurons may depend on more than the retinal stimulus: it may depend on the orientation of the animal relative to the stimulus or on the meaning of the stimulus for the animal. The former possibility is suggested by the afferent connections of inferotemporal cortex and the latter by both the behavioral effects of inferotemporal lesions and the incredible specificity of the trigger features of a few units.

Besides its input from the geniculostriate system, inferotemporal cortex (and circumstrate cortex) receives a projection from the pulvinar (3, 5) which, in turn, receives a projection from the superior colliculus (29). There is considerable evidence that the superior colliculus is implicated in visual orientation and localization (e.g., 8, 23, 31, 33, 36). Thus, it is conceivable that information about the relation of visual stimuli to the position or movement of the animal's head and eyes may be projected corticopetally from the pulvinar. That is, inferotemporal cortex (and perhaps circumstriate cortex) may integrate pattern analysis functions of the geniculostriate system with orientation functions of the tectofugal system.

The speculation that "adequacy" of a stimulus for inferotemporal neurons might also be a function of the meaning of the stimulus is similar to Konorski's (25) hypothesis of "gnostic units." It was repeatedly suggested by observing units such as the one described above that fired best to the shadow of a monkey hand. Further support for this possibility comes from the analysis of the discrimination deficit that follows inferotemporal lesions: this deficit depends on several nonsensory factors such as the animal's prior experience, the training procedure used, and the type of reinforcement (15 and e.g., 5, 17, 24, 27, 28).

In summary, the present results demonstrate that inferotemporal cortex neurons receive specific and complex visual information. The visual responsiveness of these neurons is dependent on striate cortex and they probably receive visual information over a corticocortical route from striate cortex to the circumstriate belt, and then to inferotemporal cortex. The large receptive fields of inferotemporal neurons and the specific trigger features of some of them suggest that the processing of information in inferotemporal cortex continues the trends seen in the geniculostrate system. However, it is also possible that new types of integration occur in inferotemporal cortex—that the activity of inferotemporal units depends

on more than the retinal stimulus. For example, it may also depend on information received from the tectofugal system about the location of the stimulus relative to the animal and on the significance of the stimulus for the animal. We are currently examining these possibilities in behaving monkeys.

SUMMARY

1. The responses to visual stimuli of 263 neurons in inferotemporal cortex were studied in paralyzed monkeys anesthetized with nitrous oxide and oxygen.

2. All had receptive fields that included the fovea and were relatively large. Bilateral, contralateral, and ipsilateral receptive fields were found.

3. Most neurons were sensitive to several of the following parameters of the visual stimulus: contrast, wavelength, size, shape, orientation, and direction of movement. Some had highly specific and unique trigger features.

4. The results were viewed as supporting the hypothesis that inferotemporal cortex further processes visual information received from the geniculostriate system and may be involved in additional visual functions.

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A preliminary account for some of these results has been published (16).

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