

Visual Properties of Neurons in a Polysensory Area in Superior Temporal Sulcus of the Macaque

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SUMMARY AND CONCLUSIONS

1. We recorded from single neurons in the dorsal bank and fundus of the anterior portion of the superior temporal sulcus, an area we term the superior temporal polysensory area (STP). Five macaques were studied under anesthesia (N₂O) and immobilization in repeated recording sessions.

2. Almost all of the neurons were visually responsive, and over half responded to more than one sensory modality; 21% responded to visual and auditory stimuli, 17% responded to visual and somesthetic stimuli, 17% were trimodal, and 41% were exclusively visual.

3. Almost all the visual receptive fields extended into both visual half-fields, and the majority approached the size of the visual field of the monkey, including both monocular crescents. Somesthetic receptive fields were also bilateral and usually included most of the body surface.

4. Virtually all neurons responded better to moving visual stimuli than to stationary visual stimuli, and almost half were sensitive to the direction of movement. Several classes of directional neurons were found, including *a*) neurons selective for a single direction of movement throughout their receptive field, *b*) neurons selective for directions of movement radially symmetric about the center of gaze, and *c*) neurons selective for movement in depth.

5. The majority of neurons (70%) had little or no preference for stimulus size, shape, orientation, or contrast. The minority (30%) responded best to particular stimuli. Some of these appeared to be selective for faces.

6. The properties of most STP neurons, such as large receptive fields, sensitivity to movement, insensitivity to form, and poly-

modal responsiveness, suggest that STP is more involved in orientation and spatial functions than in pattern recognition.

INTRODUCTION

The superior temporal polysensory area, or STP, lies in the upper bank and fundus of the anterior portion of the superior temporal sulcus of the macaque (12) (see Fig. 1). It is distinguishable from the surrounding cortex by its cytoarchitecture and thalamic afferents (7, 12, 18). Furthermore, unlike the surrounding cortex, STP receives a converging input from the visual, auditory, and somesthetic systems (19, 41).

In a previous study we recorded visual, auditory, and somesthetic responses from small clusters of units in STP (12). In the present paper we report on the properties of isolated single neurons in STP. Although polysensory responsiveness was common at the single neuron level, vision appeared to be the dominant modality. Consequently, we concentrated on studying visual receptive fields and visual response properties.

METHODS

Animal preparation

Four *Macaca fascicularis* and one *Macaca mulatta*, weighing 3–6 kg, were recorded from 8 to 17 times each. One week prior to recording, stainless steel wells (3-cm diameter) and a head bolt were affixed to the skull. The head bolt was used to fix the animal in a stereotaxic machine. The wells were located on the dorsal surface of the skull, with centers approximately at stereotaxic coordinates +15 mm frontal and 18 mm lateral.

The recording procedure has been described in detail by Desimone and Gross (12). Briefly, the animal was paralyzed with pancuronium bromide (Pavulon) and respired with a mixture of nitrous

oxide and oxygen (70:30). Both eyes were treated with cyclopentolate and were focused at 57 cm with contact lenses. Recording sessions lasted 10–15 h. At the end of the session the infusion of Pavulon was stopped, and when the monkey was able to breathe it was returned to its cage. At least 2 days intervened between successive recording sessions.

Recording

Single units were isolated with varnish-coated tungsten microelectrodes (5–15 μm of exposed tip, 2 to 6 M Ω impedance at 400 Hz). All electrode penetrations were oriented vertically in the coronal plane. To protect the electrodes, they were retracted inside a guide tube, which was lowered through the dura mater before the electrode was advanced.

Visual stimulation

Two categories of visual stimuli were used: rear projected and front illuminated.

Stimuli were rear projected onto a 70 x 70 cm Polacoat tangent screen 57 cm from the animal. Projected stimuli included slits of light, spots, a variety of colored slides, and shadows of various objects. The background illumination of the screen was approximately 1 mL. Light stimuli were typically 1.7 log units above and dark stimuli about 2 log units below the background. The projected stimuli were produced by hand-held projectors or by an optical bench controlled by a PDP-12 computer. Poststimulus time histograms (PSTs) for these and all other stimuli were compiled on the basis of 10–70 trials each.

The front-illuminated stimuli were presented against a black or white background that extended to the borders of the monkey's visual field. A 150-W reflector-flood lamp positioned above and behind the animal's head provided the sole light source. The luminances of the black and white backgrounds were 1 and 50 mL, respectively, and stimulus luminances ranged between these values.

Front-illuminated stimuli included white and patterned cardboard squares ranging from 0.5 to 100 cm in size, photographs of human and monkey faces, and a variety of miscellaneous objects and pictures. These stimuli were presented either manually or mechanically. The device for mechanical presentation of front-illuminated stimuli consisted of a motorized arm that swept stimuli in a circle (radius 51 cm) about the animal's head, along the horizontal or vertical meridian. Another device moved stimuli along linear paths, and was used to move stimuli directly toward or away from the monkey's head. Voltages from these devices signaled stimulus location to the computer.

Most receptive-field borders extended beyond the tangent screen and hence were plotted using front-illuminated stimuli. Stimuli were moved

along a perimeter (200° of visual angle) that could be positioned along either the horizontal or vertical meridian.

Nonvisual stimulation

Auditory stimuli included clicks, tones, jangling keys, and tape-recorded monkey calls. PSTs were compiled using free-field clicks and tones from a loudspeaker.

Somesthetic stimuli included gentle taps or stroking of the skin, manipulation of the limbs, deep pressure, and air streams. PSTs were compiled using a probe attached to a speaker coil that could be positioned anywhere on the body. A signal from the computer pulsed (20 ms) the coil, causing the probe to tap the skin beneath it.

Histology

Following the final recording session, the monkey was given an overdose of sodium pentobarbital and perfused with saline followed by buffered Formalin. Sections were stained with cresyl violet. The identification of penetrations and location of recording sites was aided by the pattern of small lesions (4 μA , 20 s) made during the recordings. Figure 1 shows representative penetrations made through different portions of STP. Penetrations older than 1 mo usually could not be identified; their location was estimated by relating their stereotaxic coordinates to those of nearby penetrations.

RESULTS

We studied 452 isolated neurons on 123 penetrations in eight hemispheres of the five monkeys. These penetrations entered the superior temporal sulcus from 2 mm posterior to the anterior end of the superior temporal sulcus to within 4 mm of the junction of the lateral sulcus with the superior temporal sulcus (see Fig. 1). All recording sites fell within the polysensory area in the dorsal bank and floor of the superior temporal sulcus previously described by Desimone and Gross (12). This area corresponds approximately to cytoarchitectonic area T3 of Jones and Burton (18) and lies anterior to the striate-projection zone in the posterior superior temporal sulcus (14, 44, 49).

Polysensory responses

Ninety-six percent of the 452 neurons were visually responsive, and over half also responded to somesthetic or auditory stimuli. Of 383 neurons tested in all three modalities, 41% responded exclusively to visual stimuli, 21% responded to visual and auditory stim-

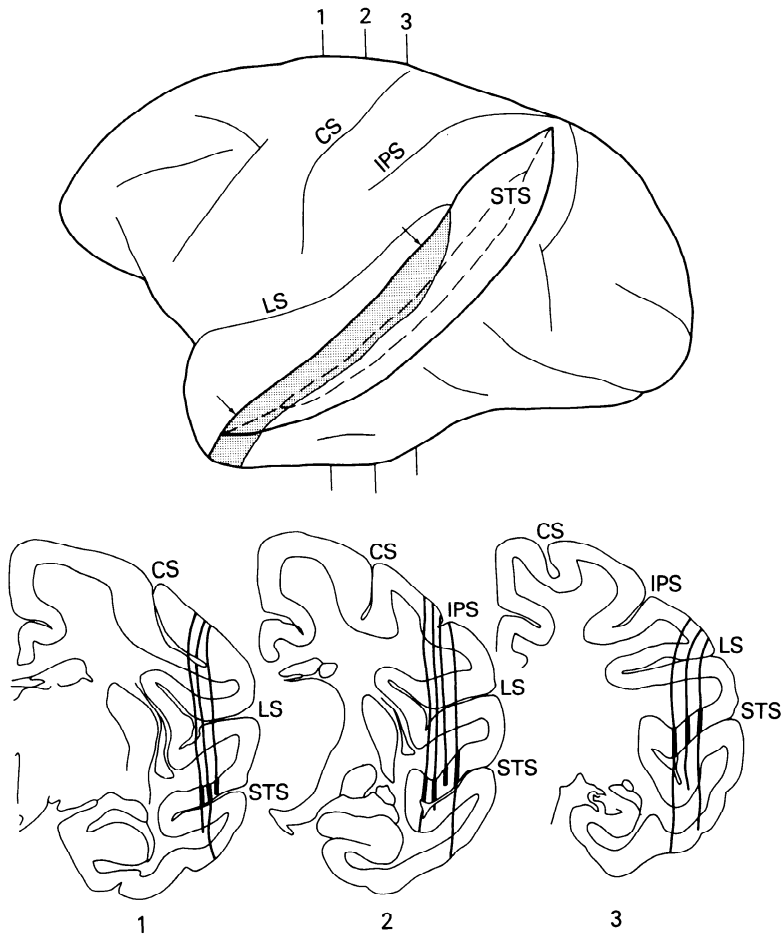


FIG. 1. Upper: lateral view of the macaque brain with the superior temporal sulcus (STS) opened up; the floor of STS is delineated by dashed lines. The superior temporal polysensory area is shaded gray. The two arrows indicate the anterior and posterior limits of the recording area. Lower: three coronal sections showing reconstructions of rows of electrode penetrations from one monkey. Intersections of penetrations with STP are indicated by thickening of the penetration lines. CS, central sulcus; IPS, intraparietal sulcus; LS, lateral sulcus; STS, superior temporal sulcus.

uli, 17% responded to visual and somesthetic stimuli, 17% were trimodal, responding to all three modalities tested, and 2% were unresponsive. With one exception, no cell responded to auditory or somesthetic stimuli in the absence of a visual response. Examples of both types of bimodal cells and of a trimodal cell are shown in Fig. 2. Since many cells responded to auditory stimuli but not to somesthetic, or vice versa, we believe the polysensory responses of STP neurons are not caused by nonspecific arousal.

Response latencies for each of the three modalities were estimated from poststimulus time histograms. Somesthetic and auditory

latencies were relatively short; the median latency of the somesthetic responses was 55 ms (24 neurons) and of the auditory responses 45 ms (27 neurons). Ninety percent of both the somesthetic and auditory latencies were under 80 ms. The latencies of the visual responses were much longer; the median latency was 140 ms (27 neurons) and none were under 90 ms.

Visual receptive-field size

Most visual receptive fields were extremely large. Almost all (92%) extended into both visual half-fields, and the majority approached the size of the visual field of the

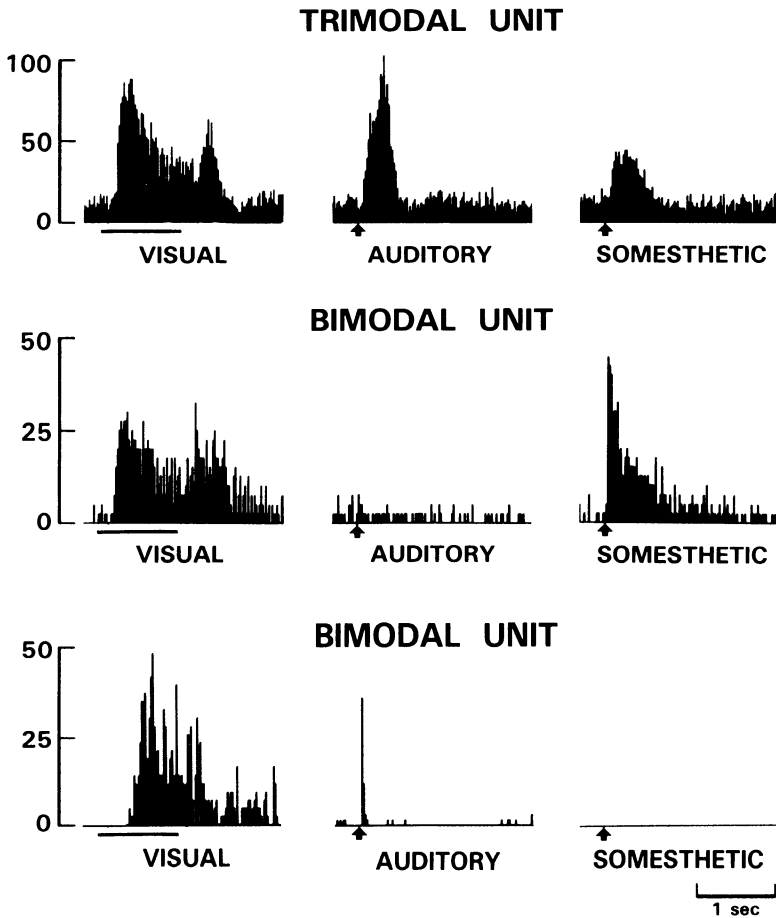


FIG. 2. Poststimulus time histograms showing responses of three STP neurons to a visual stimulus, to a click, and to a mechanical tap on the bottom of the foot. The visual stimulus for the upper and middle histograms was a vertical slit of light and for the bottom histogram, a color slide of a monkey's face. The vertical scale in this and subsequent histograms represents the number of impulses per second. The horizontal lines indicate the presentation of the visual stimuli and arrows, the presentation of the auditory and somesthetic ones.

monkey, including one or both monocular crescents. Typical receptive fields are shown in Figs. 3 and 4.

We divided a sample of 256 units into three classes based on receptive-field size. Neurons in size class 1 (80%) responded to stimuli throughout almost the entire visual field. All neurons in this class had receptive fields that extended more than 30° from the fovea in all directions; the median horizontal extent was 150° and the median vertical extent, 105° . Half the neurons in this class responded similarly throughout most of their receptive field, but 34% were more responsive in the contralateral field, 4% in the ipsilateral, and 13% at the fovea.

In size class 2, containing 14% (37) of the units, receptive fields were smaller, extending more than 30° into only one or two quadrants of the visual field. Thirty-one of these units had receptive fields predominantly in the contralateral hemifield, and 21 of these fields were entirely contralateral. Nearly all of the predominantly contralateral fields were found near the posterior border of the recording area.

Size class 3, 5% (13) of the units, had the smallest receptive fields, extending less than 30° from the fovea in any direction. In contrast to most units in the other classes, these units responded optimally to stimuli located at the fovea.

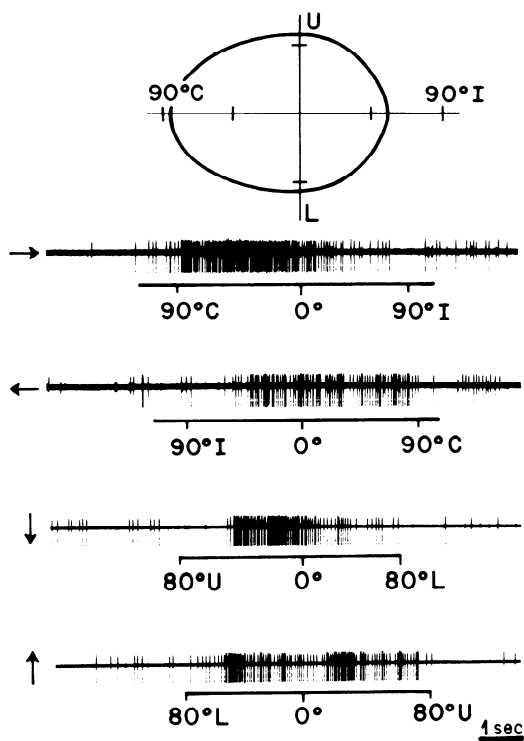


FIG. 3. Visual receptive field of an STP neuron and responses of the neuron to a stimulus moved along each of the visual-field meridians in directions indicated by arrows. In the receptive-field plot, the horizontal and vertical lines represent meridians. The stimulus was a 5° white square moved at approximately $35^\circ/\text{s}$ along a circular path about the monkey's head. Only the contralateral eye was stimulated. The scale under each trace indicates the stimulus location in degrees of visual angle. 0° represents the center of gaze; C, contralateral; I, ipsilateral; L, lower; U, upper.

The exclusively visual neurons had smaller receptive fields (classes 2 and 3) twice as frequently as the polymodal neurons (22 vs. 11%, $\chi^2 = 4.38$, $P < 0.05$).

Visual-response properties

Nearly all neurons preferred moving to static stimuli. For many units the responses were weak and rapidly habituated, and such units were not studied in detail.

DIRECTION OF MOVEMENT. Of 197 units tested, 52% showed no sensitivity to direction of stimulus movement. The remaining units responded strongly to some directions of movement and showed weaker or inhibitory responses to other directions. They fell into one of the following classes.

Direction class 1 (13%) consisted of neu-

rons that had a single preferred direction throughout their receptive field, e.g., downward. This type of direction preference was much more common (67%) among units with size class 2 (intermediate) receptive fields than either size class 1 or size class 3 (6 and 13%, respectively; $\chi^2 = 56.7$, $P < 0.001$). Furthermore, the preferred direction of movement of the cells with large bilateral receptive fields was never horizontal. Consequently, no cell preferred movement toward the vertical meridian in one hemifield and away from the vertical meridian in the other.

Direction class 2 (8%) cells responded to movement in depth, but not to movement in a plane equidistant from the monkey. Nine cells were excited by movement in depth toward the monkey and seven cells were excited by movement in depth away from the monkey. Figure 5 shows an example of a cell that was excited by movement directed away from the animal. All cells in this class had large bilateral receptive fields (size class 1), and the direction preferences were always the same throughout the receptive field and when tested with either eye.

The sensitivity to movement in depth was found under monocular viewing conditions and depended on the changing size of the retinal image (the principal monocular cue for movement in depth). The responses of these units to movement in depth were not due to changes in luminance that might accompany such movement because their movement preference was the same whether the stimulus was lighter or darker than the background and because they did not respond to the onset or offset of projected stimuli. Furthermore, these responses were not due to changes in focus because the direction preference was the same whether the movement was inside of or beyond the focal plane. Finally, units in this class that responded to a spot of light responded appropriately to its expansion or contraction; those selective for approaching stimuli responded to expansion of the spot and those selective for receding stimuli responded to its contraction.

Direction class 3 neurons (19%) had preferred directions of movement radially symmetric about the center of gaze. Half responded to stimuli moving toward the center of gaze from any place in the peripheral vi-

sual field (centripetal preference), and half responded to stimuli moving away from the center of gaze into the peripheral visual field (centrifugal preference). Unlike direction class 2 cells, these cells were not selective for movement in depth and, unlike direction class 1 cells, they did not have a single preferred direction of movement throughout their receptive field. The direction selectivity of these units was independent of stimulus contrast. All of these units had large receptive fields (size class 1). Figure 6 illustrates a unit selective for centrifugal movement.

Other units (8%) had direction preferences that did not belong exclusively in any of the above classes. For example, seven units had a combination of a movement in depth preference and a centrifugal or centripetal preference. Another three units responded to rotation of objects much better than to linear movement in any direction.

Neurons sensitive to one, two, or three modalities were distributed similarly among all classes of direction sensitivity.

TYPES OF MOVEMENT. Although smooth, continuous stimulus movement over a wide velocity range was an adequate stimulus for most units, some units responded much better to other types of movement. Twenty units responded best to jerky stimulus movements; these units gave a discrete response to each acceleration of the stimulus (see Fig. 4). Ten units responded well only to slow stimulus movement, approximately $5^\circ/\text{s}$ or less. Ten units responded to the initial appearance of a moving stimulus anywhere in the receptive field, but did not respond to any subsequent motion or changes in motion. Five units responded to stimulus disappearance in an analogous fashion. There was no significant relationship between the type of movement preference and the modality sensitivity, receptive-field size, or direction of movement preference.

For another 15 units, a person walking within the visual field was more effective than any other stimulus we tested. Informal observations suggested that the pattern of movement generated by walking and not the person per se was crucial for the response of these units. For example, a person seated in a moving chair or a person walking with the lower part of the body shielded elicited little or no response from these units. Large

inanimate moving objects also elicited little or no response. The angle subtended by the person ($20\text{--}70^\circ$) and the person's actual size and clothing were also irrelevant. Furthermore, some of these units gave discrete responses to each step of a person's movement. Half of these units responded preferentially to particular directions of walking. All had large (class 1) receptive fields.

STIMULUS PREFERENCES. Most STP units, 70% of the 199 tested, had little or no preference for stimulus size, shape, orientation, or contrast. These nonselective units would respond similarly to spots and slits of light, to shadows, to slides and photographs of complex objects, and to three-dimensional objects. Many of these units would even respond to a very small ($<1^\circ$) stimulus moving rapidly ($>50^\circ/\text{s}$) through a small portion of the peripheral visual field.

The remaining neurons (30%, 59) responded best to particular stimuli. The most interesting of these were seven units that appeared to be selective for faces. These cells responded strongly to monkey and human faces but weakly or not at all to all other visual stimuli tested, including bars, spots, edges, and complex stimuli such as hands and brushes. Three lines of evidence suggest that these units were selective for the overall configuration of a face rather than any single component. First, they responded to a variety of human and monkey faces (real faces, slides, and photographs) differing in size, color, and movement. Second, covering the eyes on the photographs reduced but did not eliminate the response. Third, scrambling the photographs eliminated the response. These properties are illustrated for one unit in Fig. 7.

These "face" cells responded best at the center of gaze but the exact stimulus location was not crucial. Most had size class 3 receptive fields similar to the one shown in Fig. 7. The visual response latencies of these cells were very long, ranging from 200 to 300 ms. (see Fig. 3).

The preferences of the remaining 52 selective units were varied. Fourteen units initially appeared selective for faces; further testing showed either that their response depended on some specific feature of the face, such as its eyes or hair, or that they would respond to other complex stimuli in addition

to faces. Seventeen units responded best to very large stimuli ($>30^\circ$). Three units responded better to long narrow slits. The remaining units responded best to particular sets of stimuli, but we were unable to characterize these preferences.

Almost half (45%) of the cells that responded exclusively to visual stimuli were selective for particular stimuli whereas only a quarter of the polymodal cells were, a significant difference ($\chi^2 = 8.72$, $P < 0.01$). (Among the visual and auditory neurons 33% were selective; among the visual and somesthetic, 25%; and among the trimodal, 18%.) Furthermore, stimulus selectivity was more common with small (class 3) receptive fields than with larger (classes 1 and 2) fields ($\chi^2 = 7.25$, $P < 0.01$).

EXCITATORY AND INHIBITORY RESPONSES. Seventy percent of the 433 visually responsive units gave only excitatory responses to visual stimuli. For 3% of the units a decrease in the spontaneous activity was the only visual response, and for 27%, the visual response could be excitatory or inhibitory, depending upon the stimulus, its location, and direction of movement.

Most of the inhibitory responses were found when stationary stimuli were presented in the central region of the visual field. Inhibition was usually stronger to large, complex stimuli in contrast to the typical lack of stimulus specificity for excitatory responses. Figure 8 shows a unit with excitatory responses to movement in the periphery and inhibitory responses to a stimulus flashed over the fovea. Figure 9 shows inhibition of a unit with a high spontaneous rate of activity and illustrates two aspects in which the inhibitory responses generally differed from excitatory responses; first, excitatory responses were similar over much of the visual field, but inhibition was optimal to centrally located stimuli and weaker or absent in the periphery. Second, excitatory responses stopped when the stimulus movement stopped, but inhibition often continued for several seconds if the stimulus remained stationary at the center of gaze.

Inhibitory responses to stimuli presented in the center of the visual field were more common among the polymodal neurons than among the exclusively visual ones (35 vs. 20%, $\chi^2 = 5.7$, $P < 0.05$), more common

among the cells with large receptive fields (size class 1) than those with smaller fields (size classes 2 and 3) (32 vs. 11%, $\chi^2 = 6.7$, $P < 0.01$), and more common among the cells with centrifugal or centripetal direction preference (direction class 3) than among the other directional or nondirectional cells (39 vs. 20%, $\chi^2 = 4.94$, $P < 0.05$).

Somesthetic and auditory response properties

Although virtually every unit was tested for somesthetic and auditory responses, these modalities were not studied as systematically as the visual. Somesthetic receptive fields were almost always large and bilateral, generally including the entire body. Usually any type of stimulus (light or deep pressure, stroking, blowing) would elicit a response. Many of the somesthetic units were extremely sensitive and some would respond to bending a single hair.

Clicks, tones, and vocalizations were all effective stimuli for most units responsive to auditory stimuli. A minority of cells responded best to certain sounds, but such preferences were not systematically studied. Most auditory units responded regardless of the location of the sound source, but a few units responded more to sounds from the contralateral side. For one unit, sounds from the contralateral side were excitatory and sounds from the ipsilateral side were inhibitory.

We occasionally observed complex interactions of visual and auditory stimuli. For example, a few neurons responded to an object striking a surface but neither to the sight or sound of the event alone, nor to the simultaneous presentation of a flash and click. Auditory-visual interactions in this region have been reported previously (3).

DISCUSSION

Afferent basis of STP polysensory responses

Anatomical experiments (19, 41) have shown that the region in the superior temporal sulcus that we term STP receives projections from inferior temporal cortex, whose neurons are visual (12, 16), from superior temporal cortex, whose neurons are auditory (16, 24), and from posterior parietal cortex, whose neurons often respond to visual or

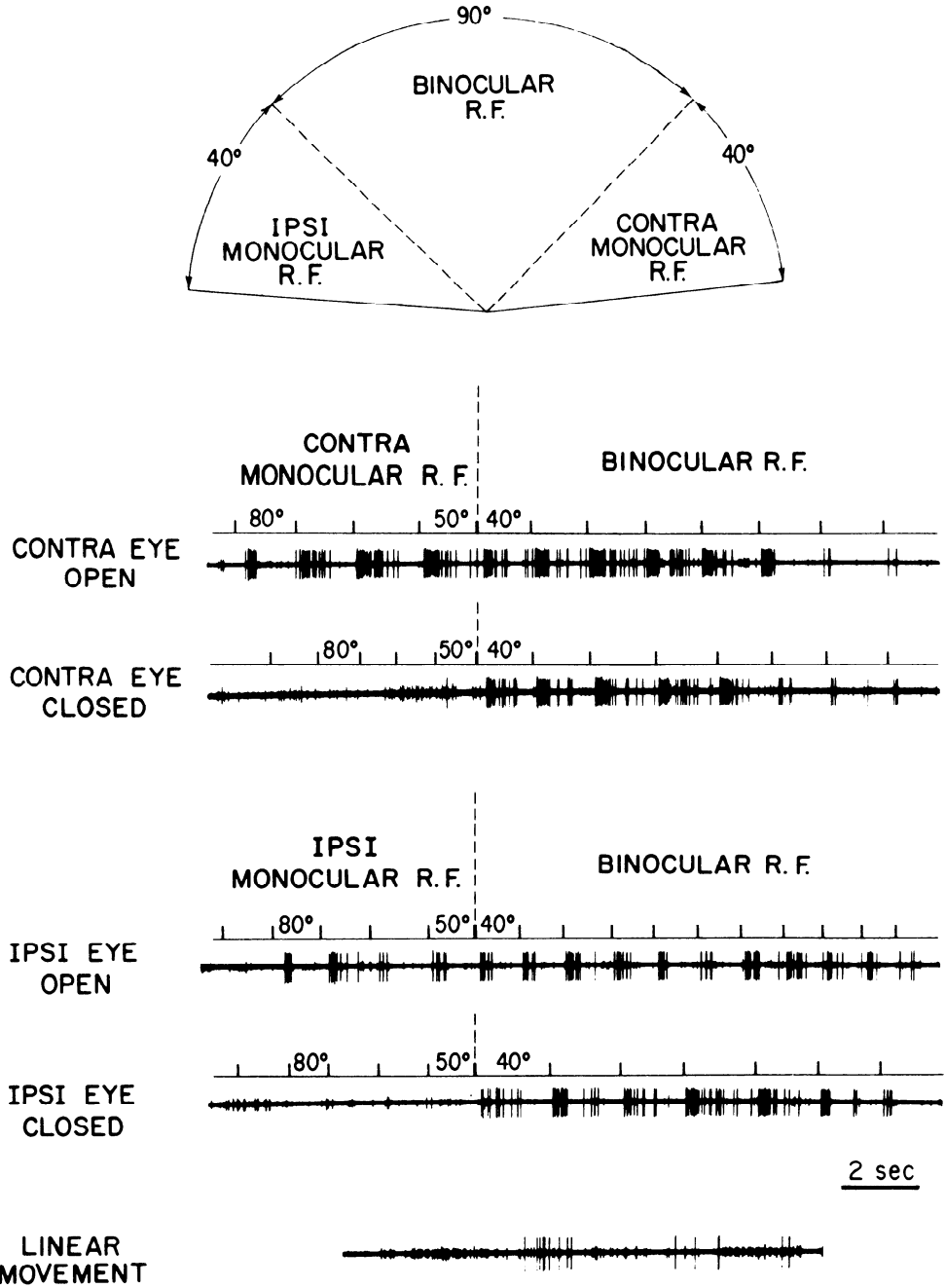


FIG. 4. Responses of an STP neuron whose receptive field extended into the monocular crescents of both eyes. The diagram shows the extent of the receptive field along the horizontal meridian of each eye. As this neuron preferred jerky movements, the stimulus was moved in discrete 10° steps indicated by ticks on scales above the unit records in the top four traces. The neuron responded to each step with a burst of spikes. The stimulus was a 5° white square moving in an arc about the monkey's head. The upper two traces were made with the stimulus starting at the extreme contralateral periphery and stepping toward the ipsilateral side. Responses beyond approximately 45° contralateral were obtained when the contralateral eye was open, as indicated by the dashed line through records and in the upper diagram. Complementary results were obtained in the ipsilateral field as shown in the third and fourth traces. The bottom trace shows the absence of a response to linear or smooth stimulus motion from 90° contralateral to 90° ipsilateral at 15°/s.

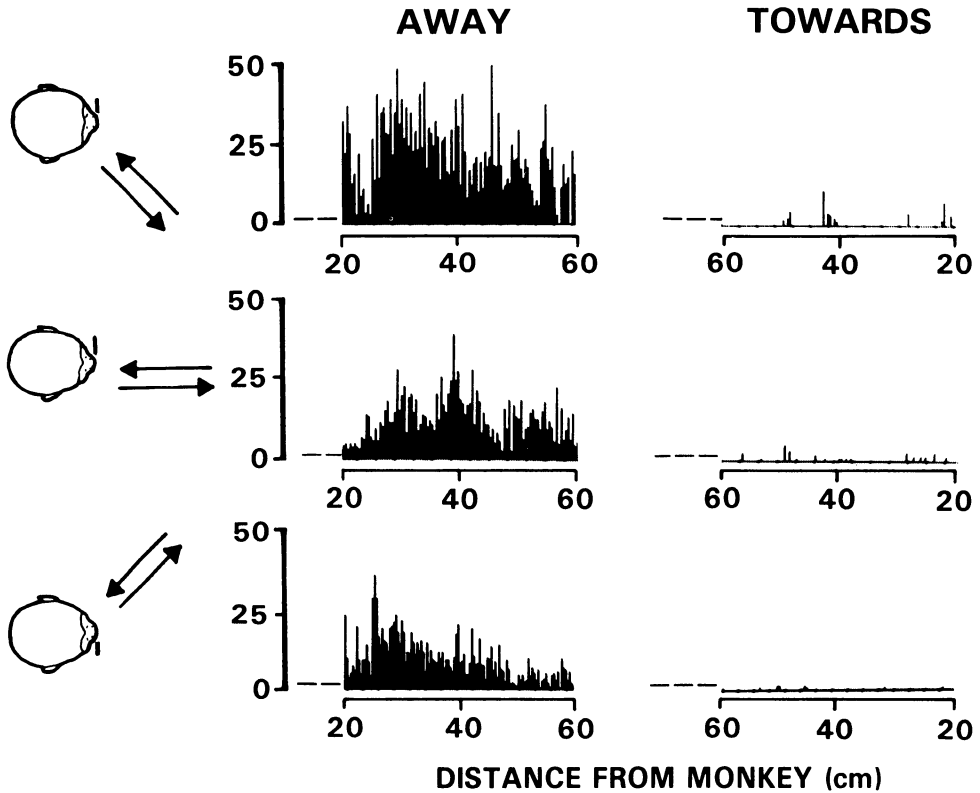


FIG. 5. Responses of an STP unit selective for stimulus movement in depth away from the animal. The unit responded to any light or dark stimulus moving away from the animal within its receptive field. In examples shown, the stimulus was a 12 x 17 cm photograph of a monkey face moved at approximately 20 cm/s along paths indicated by arrows. The dashed line indicates the mean spontaneous rate in the interstimulus intervals. One eye was occluded, as shown on the left. The receptive field of this unit extended approximately 65° into each visual hemifield.

somesthetic stimuli (28, 36). On the basis of these afferents, Jones and Powell (19) suggested that this area was a site of convergence from different sensory systems. The present results confirm this suggestion and extend previous reports of polysensory responsiveness in the superior temporal sulcus (3, 6, 12). Indeed, intermodal convergence was found at the single-unit level: about half the neurons responded to at least two modalities, and many responded to three.

It is likely that the polysensory responses we found in STP are not solely the result of converging input from inferior temporal, superior temporal, and posterior parietal cortex. We have injected STP with HRP (unpublished data) and have found that STP receives several other cortical inputs that could provide it with sensory information, viz., from lateral frontal cortex, orbital fron-

tal cortex, the cingulate gyrus, and the parahippocampal gyrus. There is evidence that each of these areas is polysensory (3, 12, 26). Thus, the sensory convergence seen in STP could have occurred elsewhere. Furthermore, STP receives projections from the medial pulvinar (7), which in turn receives projections from the deeper layers of the superior colliculus (2), in which visual, auditory, and somesthetic neurons have been found (45). In any case, inferior temporal cortex could not be the only source of visual information for STP because ablation of striate cortex eliminates the visual responses of inferior temporal neurons but does not eliminate the visual responses of STP neurons (11, 37).

Visual properties of STP neurons

Vision appeared to be the dominant modality for STP: virtually all the neurons were

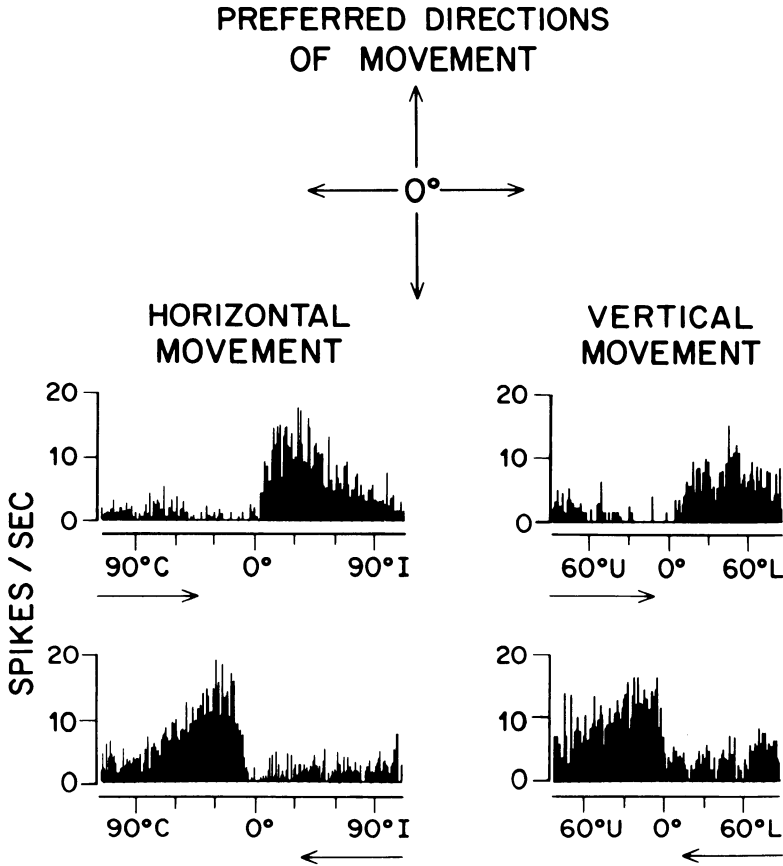


FIG. 6. Responses of an STP unit selective for centrifugal motion. The unit responded to a stimulus moving away from the center of gaze, independent of stimulus form or contrast, throughout virtually the entire visual field. Histograms show the response to a $5 \times 3^\circ$ white bar moving on a circular path around the animal's head along the horizontal or vertical meridian at $20^\circ/\text{s}$. Arrows indicate the direction of stimulus movement. Only the contralateral eye was stimulated.

visual and about half exclusively so. The great majority of STP neurons responded to visual stimuli throughout virtually the entire visual field. They were more often sensitive to specific types of movement than to the size, shape, orientation, or contrast of the stimulus. These properties suggest that they may be involved in some orientation or visuomotor functions rather than in pattern perception and recognition, i.e., in what Trevarthen (43) called ambient (as opposed to focal) vision. For example, the neurons sensitive to centrifugal or centripetal movement and those sensitive to stimuli approaching or receding in depth may play a role in analyzing the transformations of the visual world encountered during locomotion. The idea that these STP neurons may be implicated in orientation functions is also consis-

tent with their polysensory responsiveness since orientation, although primarily visual in primates, is a supramodal function.

A few STP neurons had relatively small receptive fields and responded best to specific stimuli such as faces. Other apparently similar face neurons have been reported in the floor of the superior temporal sulcus, in inferior temporal cortex, and in lateral frontal cortex (10, 30, 33). However, in this and the previous studies, the interpretation of these observations is unclear. One possibility is that they are part of a cortical system specialized for the recognition of faces or facial expressions. In man, a selective impairment in the recognition of faces (prosopagnosia) is associated with temporal lobe damage (23). Another possibility is that the responses of these neurons are correlates of

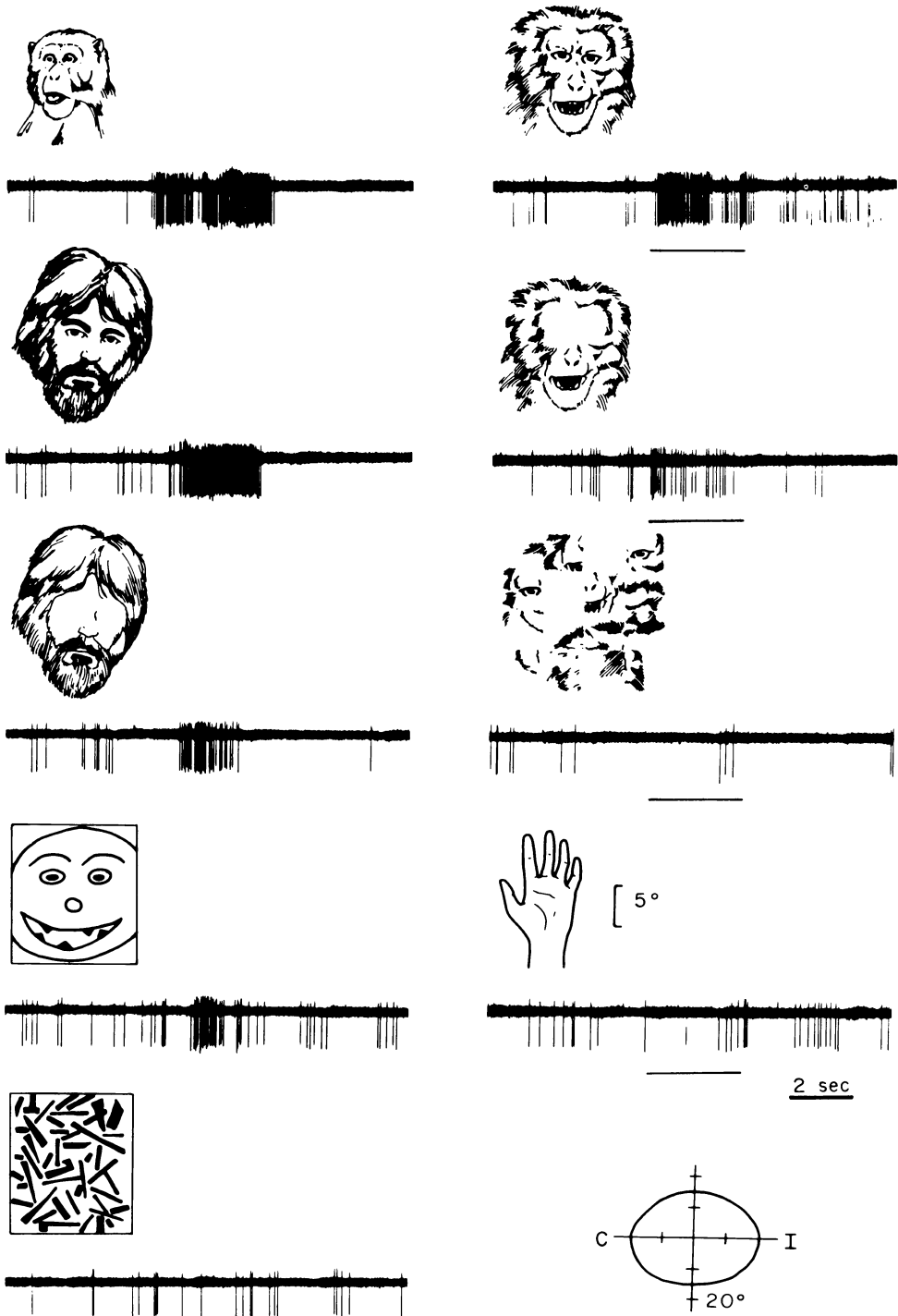


FIG. 7. Responses of an STP unit that responded better to faces than to all other stimuli tested. Removing eyes on a picture or representing the face as a caricature reduced the response. Cutting the picture into 16 pieces and rearranging pieces eliminated the response. Stimuli represented on the left were traced from a color photograph (monkey face), black and white photographs (human face), and drawings (caricature and random pattern), which were swept across the fovea at $10^\circ/\text{s}$. Stimuli represented on the right were traced from color slides, which were projected on the fovea for 3 s, indicated by the horizontal bars. All the unit records are representative ones chosen from a larger number of trials. The receptive field is illustrated on the lower right.

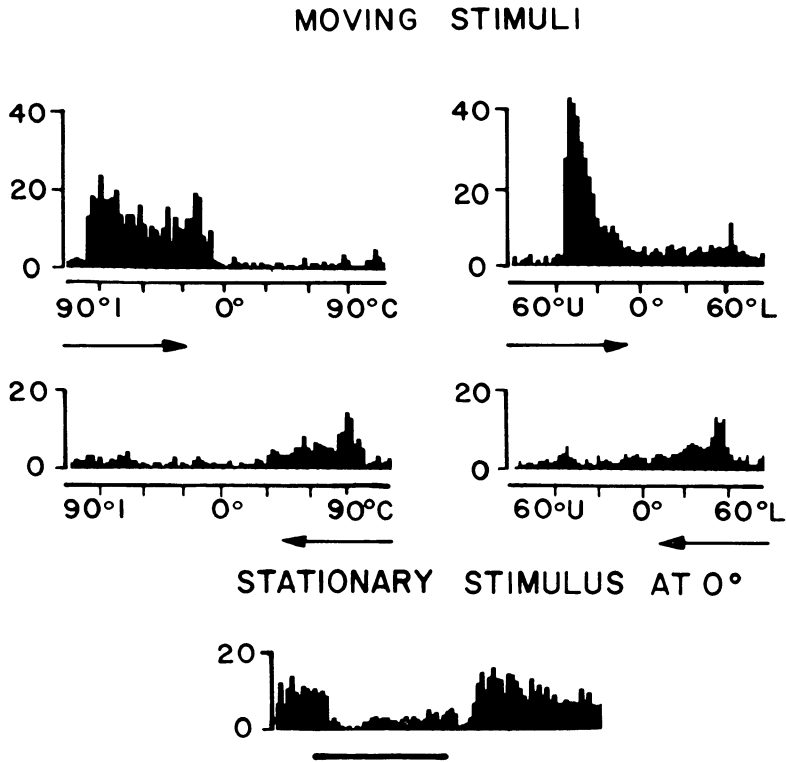


FIG. 8. Responses of an STP unit that was excited by stimulus movement in the periphery and inhibited by complex stimuli presented at the center of gaze. Upper: four histograms show the excitatory responses of the unit to a stimulus moved along the horizontal or vertical meridian in directions indicated by arrows. The stimulus was a bar moving in an arc about the monkey's head at approximately $22^\circ/\text{s}$. Lower: activity of the same unit is suppressed during the presentation of a color slide of a monkey face at the center of gaze. In order to better demonstrate the suppression, the activity of the unit was increased by moving another stimulus in the periphery throughout each trial. The horizontal line indicates the 1 s duration of the central stationary stimulus.

certain motor responses (grimaces, calls) typically evoked by faces. Finally, we cannot exclude the possibility that these neurons may be equally responsive to other, nonface stimuli that were not tested.

Comparison with other areas

Some insight into the possible functions of the superior temporal polysensory area may be obtained by comparing it with other cortical visual areas. The properties of STP appear to be rather different from those of inferior temporal cortex, but similar to many visual properties of frontal and parietal cortex. With respect to striate and prestriate cortex, STP appears to represent an elaboration of the directional properties but to have little relation to other well-known fea-

tures of these areas, such as selectivity for stimulus color and orientation.

STRIATE AND PRESTRIATE CORTEX. Neurons in striate and prestriate cortex have discrete visual receptive fields that are organized to form topographic representations of the contralateral visual field (1, 14, 46). By contrast, STP receptive fields are extremely large and not topographically organized. For example, the median receptive-field width in striate cortex is less than 1° (40), whereas 80% of the receptive fields in STP (size class 1) are more than 150° wide and extend more than 30° into the ipsilateral visual field. As Kuffler (20) observed, the receptive-field concept may not be relevant for neurons with such extremely large response fields. Likewise, striate and prestriate neurons are often sensitive to the orientation,

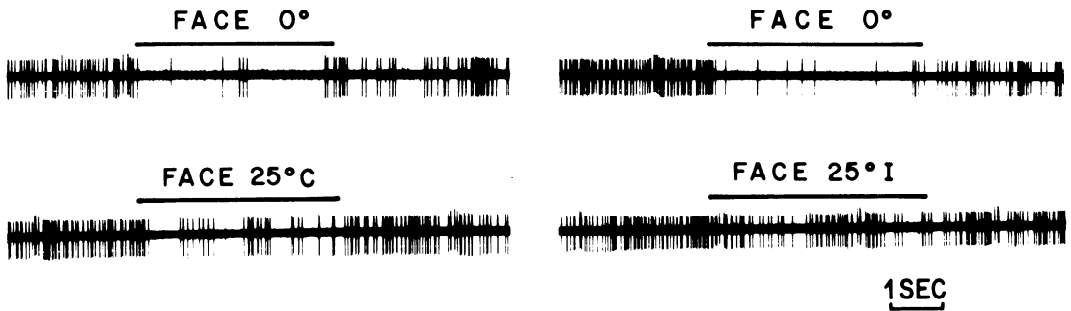


FIG. 9. Example of an STP unit that exhibited sustained inhibition to complex stationary stimuli presented at the center of gaze (0°). The horizontal lines indicate presentation of the stimulus (which was a face in this case). Note that the inhibitory response was much greater when the center of the stimulus was presented over the center of gaze than in either the contralateral (C) or ipsilateral (I) field.

size, and color of the stimulus (51), whereas STP neurons are rarely sensitive to these parameters. All these differences indicate that STP, unlike striate and prestriate cortex, probably does not play an essential role in form vision.

There is one important property, namely, direction selectivity, which is common to neurons in STP, striate, and prestriate cortex. While some aspects of directional selectivity in STP have clear counterparts in striate and prestriate cortex, other aspects do not.

Direction class 1 neurons in STP are similar to most directionally selective cells in striate and prestriate cortex in having a single preferred direction of movement in a plane equidistant from the eye. They differ primarily in receptive-field size; the STP neurons respond to a single direction throughout much of the visual field.

Direction class 3 neurons in STP, selective for directions of movement radially symmetric about the center of gaze, i.e., centripetal or centrifugal motion, have no obvious counterpart in striate or prestriate cortex. The only other areas where similar neurons have been described is posterior parietal cortex (27).

Direction class 2 neurons in STP are selective for movement in depth, and this selectivity is based on the expansion or contraction of the retinal image of the stimulus. Neurons sensitive to changing size have been reported in the striate-projection zone of the posterior superior temporal sulcus in the monkey (50) and in area 18 of the cat (35).

Unlike the STP neurons, these prestriate neurons require an opposed movement of two edges with a certain contrast, orientation, and retinal location. By contrast, the response of STP neurons to changing size is independent of these parameters and thus provides more generalized information about movement in depth than prestriate neurons do.

Neurons in striate and prestriate cortex have also been reported to respond to changing binocular disparity (8, 32, 42), the stereoscopic cue for movement in depth. Psychophysical experiments indicate that both changing size and changing disparity information converge onto a general "motion-in-depth stage" (34). Whether STP neurons respond to changing disparity as well as to changing size remains to be tested.

The directional neurons in striate and prestriate cortex are probably the basis for the directional properties of STP neurons. Indeed, we recently found that removal of striate cortex eliminates all classes of directional selectivity in STP even though visual responsiveness is not eliminated (11). Since neither striate cortex nor striate-recipient cortex projects directly to STP, the pathway must be a multisynaptic one, possibly involving several prestriate areas and the pulvinar.

INFERIOR TEMPORAL CORTEX. Inferior temporal cortex is similar to STP in not being visuotopically organized and in having many receptive fields that extend well into both visual half-fields (12, 15). In other re-

spects, however, most STP neurons have quite different properties from those in inferior temporal cortex. STP receptive fields are much larger than inferior temporal cortex fields (median sizes: $150 \times 105^\circ$ vs. $25 \times 25^\circ$) and more often bilateral (92 vs. 60%). Whereas most STP neurons respond similarly throughout their receptive fields, most inferior temporal neurons respond more strongly at the center of gaze. Furthermore, unlike the majority of STP neurons, inferior temporal neurons respond only to visual stimuli and are often sensitive to such visual parameters as shape, texture, and color (10, 15). Finally, the visual responsiveness of inferior temporal cortex is totally dependent on striate cortex (37) but much of the visual responsiveness in STP survives striate removal (11).

Lesions of inferior temporal cortex produce a severe visual learning deficit but neither sensory neglect nor deficient visuomotor performance (13). By contrast, lesions of the superior temporal sulcus that include most of STP produce both a supramodal neglect syndrome and an impairment on a task requiring visuomotor coordination while leaving visual discrimination learning unimpaired (31).

Inferior temporal cortex, and parts of prestriate cortex, form part of a cortical visual system involved in pattern recognition. The differences between the neural properties in inferior temporal cortex and STP and the contrasting effect of their removal suggest that the majority of STP neurons are not a further extension of that system.

FRONTAL AND POSTERIOR PARIETAL CORTEX. Visually responsive neurons in posterior parietal and frontal cortex are similar to most STP neurons in having large receptive fields and being insensitive to stimulus form, orientation, and color (3, 26, 28, 36, 48). Moreover, several of the unusual sensitivities of STP neurons have also been found in these areas. Neurons selective for centripetal and centrifugal movement are found in posterior parietal cortex (27). Neurons that are excited by peripheral stimuli but inhibited by stimuli at the fovea are found in posterior parietal and orbital frontal cortex (3, 48). Neurons sensitive to movement in depth are found in lateral frontal cortex (33). Polysensory neurons responsive

to somesthetic or auditory stimuli as well as visual are found in posterior parietal, lateral frontal, and orbital frontal cortex (3, 4, 26, 28, 39).

Both posterior parietal and frontal cortex lesions produce neglect syndromes and disturbances in visuospatial and visuomotor tasks, but leave visual discrimination learning unaltered (17, 21, 22, 38). As mentioned above, STP lesions appear to have similar effects. Furthermore, posterior parietal, lateral frontal, and orbital frontal cortex are all reciprocally connected with STP and, like STP, these areas receive projections from the medial pulvinar (5, 7, 14, 25, 29).

In summary, the similarity in neuronal properties of visually responsive neurons in STP, frontal, and posterior parietal cortex, the similar behavioral effects of their removal and their anatomical interconnections, all suggest that they may have functions in common or form part of an interacting system. Unlike inferior temporal cortex, most neurons in these areas do not appear to be concerned with pattern perception. Rather, they may be involved in visuomotor and visuospatial functions: in translating vision into action. One of the strongest supports for this generalization in the case of the frontal eye fields and posterior parietal cortex is that in behaving animals the activity of single neurons is often related to eye or limb movements (28, 36, 47). It would be interesting to see if this were also the case for STP.

ACKNOWLEDGMENTS

We are very grateful to Victoria Ingalls for help with histology.

Support for this work was provided by National Science Foundation Grant BNS-75-23634, National Institutes of Health Grant MH-19420, National Institutes of Health Postdoctoral Fellowship NS-05804 to C. Bruce, and National Science Foundation Postdoctoral Fellowship SPI-7914804 to R. Desimone.

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Received 3 July 1980; accepted in final form 23 March 1981.

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