Visual Responses of Inferior Temporal Neurons in Awake Rhesus Monkey

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SUMMARY AND CONCLUSIONS

1. We studied the responses to visual stimuli of neurons in area TE of the inferior temporal (IT) cortex in four awake monkeys (*Macaca mulatta*) trained to perform behavioral tasks.

2. While the monkey looked at a fixation point in order to detect its dimming, another stimulus, such as a spot of light or a sine- or square-wave grating, usually produced only slight responses in inferior temporal neurons. However, the response to the stimulus was more vigorous if the task was changed so the fixation point blinked off before the stimulus came on while the monkey maintained its gaze.

3. Responses to visual stimuli during this blink task were seen in 199 of 288 cells studied, and nearly all responded to a visual stimulus better during the blink task than during the task in which the fixation point remained on. Small spots of light usually produced consistent responses; we did not explore the response to complex stimuli or to objects. Latency of the visual response ranged from 70 to 220 ms.

4. While the response of cells to a stimulus in the presence of the fixation point was limited to areas near the fovea, this apparently constricted visual receptive field expanded during the blink of the fixation point.

5. In order to determine whether the increased response of the cell in the absence of the fixation point was due to a shift of attention from the fixation point to the visual stimulus, we required the monkey to respond to the dimming of this stimulus rather than to the dimming of the fixation point. We found that attention to the visual stimulus decreased the response of the cell during both the fixation and blink tasks. That is, the best response to the stimulus occurred in the blink task when attention to the stimulus was not required, while the poorest response occurred in the fixation task when attention to the stimulus was required.

6. The reappearance of the fixation point during stimulation presentation in the blink task caused a transient time-locked suppression of response to the stimulus. This suggests that the reduction of response to the stimulus in the presence of the fixation point is caused by an interaction between the responses to the fixation point and the visual stimulus.

7. To ensure that we were recording from the same population of cells that had first been characterized by Gross, Rocha-Miranda, and Bender (14) in anesthetized, paralyzed monkeys, we recorded under those same conditions in two of our four monkeys. The responses we found were similar to those reported originally and in general were similar to those seen in the awake monkey during the blink task. Specifically, the receptive fields were large, always included the fovea, and extended into the ipsilateral visual field. Some cells responded better to complex stimuli such as brushes than to spots of light.

8. Our experiments indicate that visual fixation and visual attention are influences that in the awake monkey alter the responsiveness of inferior temporal neurons to visual stimuli. These effects seem unlikely to be a laboratory artifact since fixation on visual objects and attention to them is such a frequent occurrence in normal vision. These two influences show that the contribution of inferior temporal neurons to visually guided
behavior cannot be understood only in terms of their visual response properties, but the visual situation and attentional state of the monkey must be considered as well.

**INTRODUCTION**

Two sets of experimental findings, one behavioral and one physiological, led to our study of single-cell responses to visual stimuli in the inferior temporal cortex of awake behaving rhesus monkeys. First, ablation of area TE (3) of the inferior temporal cortex produces lasting defects in a monkey’s ability to learn visual discriminations while leaving intact the ability to learn discriminations in other modalities (12, 22, 23). Second, inferior temporal cells have different stimulus requirements and receptive-field characteristics than single cells in other parts of the visual system (6, 14). The visually responsive inferior temporal cells studied in anesthetized, paralyzed monkeys have receptive fields that nearly always include the fovea and a large part of the contralateral visual field and usually extend into the ipsilateral visual field as well. The visual responses within these large fields are always greatest in the region of the fovea. The most effective stimuli for activating a substantial proportion of these cells have been real objects, including hands or brushes (6, 14, 35) or faces (26), rather than the more conventional spots, bars, or slits. The characteristics described for these cells apply to cells throughout area TE (6). Subsequent experiments showed that many inferior temporal cortex neurons changed their discharge rate when monkeys perform visual discrimination or visual memory tasks (10, 13, 21, 31, 32, 36).

Since the analysis of the visual responses of inferior temporal neurons has been performed using either paralyzed, anesthetized monkeys or awake monkeys in which the retinal locus of visual stimulation was uncontrolled, we attempted to study this area in awake behaving monkeys that had been trained to fixate. Our initial goal was to concentrate on the stimulus properties needed to activate the cells. We soon found that while the monkey was fixating his gaze on a small fixation point, we were able to elicit few responses from inferior temporal cells. These cells did respond, however, when the stimulus was presented in the absence of a fixation point, and our subsequent experiments concentrated on defining how the fixation point influenced the responses to other visual stimuli.

Brief reports of these experiments have appeared previously (28–30).

**METHODS**

**Procedures in awake monkeys**

Single-cell recordings were obtained from inferior temporal cortex in four monkeys (*Macaca mulatta*). The monkeys were trained to fixate a spot of light on a screen in front of them (38). When they depressed a bar, the spot came on for several seconds and then dimmed briefly; they were rewarded with a drop of water if they released the bar during the dim period. While they were fixating the spot, another visual stimulus came on, and it was this visual stimulus that we varied in order to activate the inferior temporal cells under study. The visual stimulus was usually a slit of light projected on the screen in front of the monkey and could be varied in length, width, and orientation. Stimuli were about 10°/m² on a background of about 1 cd/m². Alternatively, sine- or square-wave gratings could be presented on an oscilloscope screen on which a spot for fixation was superimposed. This task will be referred to as the fixation task (Fig. 1). All animals learned this task first and received extensive overtraining before other behavioral variations were introduced.

In order to determine the effect of the fixation point on the visual response of cells we used a “blink” task (Fig. 1). This task required the monkey to continue looking at the location of the fixation point even though the fixation point went out (the blink) 150–400 ms before the stimulus came on. After the stimulus went off, the fixation point came on again, and the monkey was rewarded for detecting the dimming of the fixation point.

In order to determine the effect of the monkeys’ use of or attention to the stimulus, we modified the fixation and blink tasks. In both modified tasks, the stimulus rather than the fixation point dimmed and the monkey was rewarded for detecting this dimming. In the blink plus stimulus attention task, the fixation spot returned 300 ms after the onset of the stimulus in order to help the monkey suppress a saccade to the soon-to-dim stimulus.

Throughout the experiments eye position was monitored using the magnetic search coil technique (17, 34). If the monkey’s eyes strayed further than 0.5–1° from the position of the fixation point while the monkey was fixating, the trial was terminated automatically by the computer, which
was controlling the experiment (18). Only data from trials in which the monkey successfully obtained a reward were used for data analysis.

Devices for restraint of the head and recording of single cells (7) and the eye coil were implanted when the monkey was anesthetized with sodium pentobarbital. In the early experiments, glass-coated platinum microelectrodes, which penetrated the dura directly and whose location was changed daily, were used for recording. Later in the series of experiments, thin-wire tungsten microelectrodes (Frederick Haer) were inserted into the brain through guide tubes placed through the dura to a depth calculated to be 5–8 mm above the cortex of interest. The guide tube was typically left in place for 3–7 days, and usually two to five penetrations were made before the guide tube was removed and placed in a new position. The shaft was slightly bent so that by rotating the electrode it exited the guide tube in different directions on successive penetrations.

In the first monkey, the recording cylinder was placed on the side of the skull to allow direct access to the inferior temporal cortex. In the subsequent three monkeys, the cylinder was placed at stereotaxic location AP +17 mm, L22 mm. With the cylinder in the latter position, we found that when the cells on the dorsal surface of the neocortex responded to stimulation of the lips or inside of the mouth, the cylinder was invariably above the region of inferior temporal cortex from which we wished to record. In the monkeys in which the penetrations were in the stereotaxic plane, IT cortex was reached at a depth of about 2.5 cm from the cortical surface. To reach that depth, the electrode passed through four successive banks of cortex, each bank of which could be driven by different stimuli. These stimuli were in order: oral movement or touch, neck or shoulder touch, auditory, and finally somatosensory and/or visual (usually rather weak responses). The fifth and sixth banks of cortex were the ones from which we recorded (area TE).

The location of recording was confirmed by passing 5–10 μA of current for 30–60 s through the microelectrode. At the end of the series of experiments, the monkeys were anesthetized and then perfused with saline followed by Formalin. Histological sections were stained with cresyl violet and the location of the guide tubes and the electrolytic lesions were determined.

The single-unit discharges were isolated on the basis of spike amplitude with an amplitude discriminator and converted to pulses. The unit pulses and all control and behavioral events were monitored by the on-line computer with a time resolution of 1 ms. The results of the experiment were monitored on-line by several displays, e.g., cell discharge, eye position, and behavioral sequence. Digital event and eye-position data were stored on disks for subsequent analysis. Two software systems, both developed within the laboratory, were used in the course of these experiments for real-time data acquisition and control (11, 15).

Quantitative comparisons of the responses of 32 cells under different experimental conditions were made from data collected in blocks of consecutive trials. The number of spikes occurring in a period after stimulus onset (usually 150 ms) were counted. The difference between the number in this period and that in an equal period prior to stimulus onset was taken as the response to the stimulus onset. These differences were ranked and then tested using the nonparametric Kruskall-Wallis test, which was chosen in order to avoid assumptions about the variances and time independence of the samples.

**Procedures in anesthetized paralyzed monkeys**

We studied area TE again in two of the monkeys used in the experiments described above while they were anesthetized and paralyzed. The monkeys were premedicated with diazepam (1
mg/kg), atropine (1.6 mg/kg), and ketamine (0.3 mg) given subcutaneously. The throat was then anesthesitized with benzocaine, and the monkey was intubated and then anesthetized with nitrous oxide. The monkeys were paralyzed with 1.5 mg of pancuronium bromide (Pavulon) and artificially ventilated at 16 strokes/min. Paralysis was maintained by subcutaneous infusion of pancuronium at 1.5 mg/h. The monkey's head was held by the same head holder used to restrain the head when the animal was awake. Body temperature was monitored and adjusted with a heating pad when necessary. End-tidal carbon dioxide was maintained between 4 and 5%. Pupils were dilated, corrective contact lenses were used to bring stimuli on a screen 114 cm in front of the monkey into focus on the retina, and the location of the fovea and optic disk for each eye was mapped onto the screen with a reversing ophthalmoscope. At the end of the experiment the infusion of pancuronium was stopped and atropine and ketamine again administered. When the monkey had recovered from paralysis enough to maintain its own breathing, its throat was thoroughly cleaned, neostigmine was administered, and the monkey was returned to its home cage.

RESULTS

We recorded from 288 cells in four monkeys. Of these, 69% (199 cells) could be activated by visual stimuli under appropriate conditions, and subsequent analysis is based on these cells. Figure 2A illustrates the area of the inferior temporal cortex where our sample of cells was located. Penetrations were in the middle and anterior parts of the temporal lobe and clearly within area TE of von Bonin and Bailey (3) (stippled area in Fig. 2A and B). The vertical lines in Fig. 2A show the location of the diagrammatic coronal section in Fig. 2B. The hatching in both sections indicates the region in which our recordings were made. A mark at one recording site is shown on the coronal section in Fig. 2C.

Effect of visual fixation on visual response

Attempts to activate cells in inferior temporal cortex while the monkey was performing the visual fixation task were only marginally successful. Figure 3 upper records, shows an example of the response of a cell to a spot of light. The cell shows a slight response to the onset of the stimulus (shown as line S), which came on while the monkey looked at the fixation point (fine F). The raster shows the individual discharges of the neuron on each trial aligned with the time of the stimulus onset, and the histogram shows the summed response of the individual trials depicted on the raster. Other stimuli such as slits of light, sine- or square-wave gratings, and the shadows of objects such as brushes (which could be presented instantaneously by placing the object in the stimulus light path), also produced responses that were weak and irregular. When the objects themselves were presented, this frequently led to an overall increase in the discharge rate of a cell but, since the monkeys became agitated by this procedure, we do not know if the increase was due to the visual stimulus or general arousal.

We noticed, however, that the cells often showed bursts of discharges when the monkey was free to look about the room between the periods of visual fixation. The bursts suggested either that we were using inappropriate stimuli or that fixation on the spot was suppressing the response to the stimuli we were using. To test the effect of fixation we made an alteration in the fixation task; the stimulus was presented when the fixation point was absent. We did this by blinking off the fixation point for 1,000–1,500 ms. During this blink of the fixation point, the monkey was required to maintain fixation for the trial to continue.

Figure 3, lower records, illustrates the remarkable improvement in the response when the stimulus was presented in this changed paradigm. The response of the cell to the stimulus presented during the blink had a higher discharge rate for a longer period of time (Fig. 3, lower records) than when the fixation point remained on (Fig. 3, upper records).

The improvement in response to the stimulus occurred whether or not the cell gave a clear response to the onset of the fixation point. The cell shown in Fig. 3 had little response to the fixation point. Other cells, such as the one illustrated in Fig. 4, showed a clear response to the fixation point at the beginning of the trial as well as when the fixation point reappeared after the blink period. For both cells the response to the stimulus in the blink task was better than that in the fixation task.
FIG. 2. Areas of inferior temporal cortex studied in five monkeys. A: region of the cortex in which the recordings were made is shown in this lateral view of the monkey brain by the cross-hatched region. The stippled area indicates the approximate extent of von Bonin and Bailey’s (3) area TE. B: coronal section through the center of the region from which recordings were made indicating area TE and the recording region. This section is 12.5 mm anterior to the interaural coronal plane; its anterior-posterior position is shown by the vertical lines above and below the diagram in A. C: electrode tracks and electrolytic lesion at inset shown in B (monkey 068).

Of the cells in inferior temporal cortex that responded to our visual stimuli, about 25% showed a decrease in discharge rate in response to a visual stimulus rather than an increase. An example of such a response is shown in Fig. 5. This decrease also is clearer in the blink than in the fixation task.

In these experiments we did not search for optimal stimulus parameters but small spots of light were usually adequate stimuli for the cells, as is shown in Figs. 3–5. An adequate stimulus size for about 60% of the responsive cells was a spot of light 3° or less in diameter. Only a few cells required a stimulus with specific length, width, and size to elicit a vigorous or consistent response. The latency of the responses to the visual stimuli ranged from 70 ms in some cells to 220 ms in other
For a few cells movement of the stimulus elicited a stronger response than a stationary stimulus. Expansion of the spot was occasionally the effective stimulus but, again, the response was better when the stimulus was presented during the blink task as shown in Fig. 6.

We compared the response of the 199 cells to a visual stimulus in the fixation and the blink tasks. For all but two cells the response to the stimulus was improved during the blink of the fixation point. For some cells, when the visual stimulus was located at the fovea, the response to the visual stimulus during the fixation task was sufficiently strong that no significant improvement occurred during the blink task. For these same cells, when the stimulus was placed in other lo-

cells; 60% of the cells had a latency of less than 120 ms. The latency did not change with changes in task.

FIG. 3. Response to a stimulus presented in the presence (upper records) and absence (lower records) of the fixation point. In the upper record the monkey was looking at the fixation point when the stimulus came on. In the lower record the fixation point went off for 1 s, during which the stimulus came on; the response is more vigorous with the fixation point off. The monkey was required to maintain gaze while the fixation point was off, and in this part of the figure only those trials are included during which the monkey's eye position deviated from the fixation spot by less than 1°. In this and subsequent figures, F indicates fixation point, S indicates stimulus; upward deflection means on, downward deflection means off. Drawings at the top indicate position and size of the stimulus in relation to the fixation point (the dot). The part of the figure to the left of fixation always represents the contralateral visual field (except Fig. 13). Dots on the raster indicate individual action potentials of the cell; successive lines show effect of stimulus presentations on successive trials. Histograms are summed from these rasters, bin width is 4 ms, and the histogram scale indicates 100 spikes/s per trial. The vertical lines across the raster and histogram are 1) onset of the fixation point on the left and 2) onset of the stimulus on the right. The monkey number (first three digits or first two letters) and cell number (remaining digits) are in the lower left corner, and the interval between dots on the time line is indicated in the lower right corner.

FIG. 4. Discharge of a cell that responded to the onset of the fixation point. The response to the visual stimulation was improved during the blink task (lower records) as compared to the fixation task (upper records). Note the on-response of the cell to the fixation point both when it first came on and when it reappeared after the blink period in the lower records. Since a saccade was probably made to the fixation point after it came on at the beginning of the trial, this on-response is not necessarily to a stimulus falling on the fovea, as is the on-response to the fixation point when it reappears.
of the response with the occurrence of saccades on a trial-by-trial basis. Resolution of the eye-position record was 10° of arc in the early experiments and 2° of arc in later experiments, and at these levels of resolution no relationship between saccades and the onset of the response of the cell could be seen (Fig. 7). The role of either smaller saccades (19) or the slow control system was not studied.

In these experiments the monkey viewed the target screen binocularly. Another possible explanation for the improved response during

![FIG. 5. More pronounced decrease of discharge rate in response to a stimulus during blink of the fixation point (lower records) than during the fixation task (upper records).](image)

**Analysis of blink effect**

The increased responsiveness of inferior temporal cells to visual stimuli during a blink of the fixation point could be the result of a number of factors. Removal of the fixation point could stimulate an eye movement, which in turn could move the visual stimulus and possibly make it more effective. While changes in eye position greater than 0.5–1.0° of arc would have terminated the trial, smaller changes in eye position would not. To determine whether small saccades could be responsible for the improved response during the blink task, we compared the vigor

![FIG. 6. Response of a cell to an expanding stimulus. Stimulus was centered on the receptive field of the cell and expanded from 0.25° to 3° during the 400 ms stimulus duration. Fixation and blink tasks as in preceding figures.](image)
the blink of the fixation point was that a change in accommodation-vergence occurred with removal of the fixation point, and this effectively produced a different stimulus during the blink either by blurring the image or by changing the disparity of the images falling on the retinas of the two eyes. If such a change in accommodation-vergence had occurred, it would have been registered as a change in eye position. The eye-position records showed no alterations consistent with any change in accommodation-vergence. In addition, we tested
five cells under both monocular and binocular viewing conditions. There was no difference in response of these cells when viewed under these conditions.

Still another possible cause of the improved response during the blink of the fixation point might have been a shift of the monkey's attention to the stimulus from the fixation point as the fixation point went off. Such a shift of attention in the absence of eye movement has been demonstrated to produce an enhanced visual response to another region of monkey cerebral cortex, the parietal lobe (5). In our blink and fixation tasks it was not possible to know to what extent the monkey shifted its attention to the stimulus, since it always responded to the dimming of the fixation point. Therefore, we modified our tasks to require the monkey to release the bar when the stimulus dimmed. If it responded correctly to the dimming of the stimulus, we infer that he must have attended to it. This attention task was combined with both the fixation and the blink task (Fig. 1, lower two paradigms). Trials on a given task were run in blocks of at least 20 so that the monkey consistently performed a task at a time. By comparing the responses of cells in the blink task with those in the blink plus stimulus attention task and in the fixation task with those in the fixation plus stimulus attention task, we could assess the influence of the monkey's directed attention.

The neuronal responses to the visual stimulus were reduced during the behavioral tasks that required the monkey to respond to the dimming of the stimulus as compared to dimming of the fixation point. This can be seen in Figs. 8 and 9 by comparing the raster and histograms across the individual rows; those on the left required no attention to the stimulus, while those on the right did. In addition, the suppressive effect of attention is more marked in the blink tasks (upper row) than in the fixation tasks (lower row), though it is present in both types of tasks. Figures 8 and 9 also show that the response to the visual stimulus is strongest in the blink task in which the influence both of the fixation point and of attention to the stimulus are absent (upper left), while the response is weakest when both influences are present (lower right). The response strength in the blink plus attention task (upper right) and the fixation plus no attention task (lower left) fell between these extremes.

In Fig. 8, the cell did not respond to the fixation point itself (note the lack of response to the reappearance of the fixation point in the blink task in the upper-left panel), while the cell shown in Fig. 9 did respond to the fixation point (note the response with fixation point reappearance). For both of the cells illustrated in Fig. 8 and 9 the response to the onset of the stimulus was reduced in the fixation as compared to the blink tasks. Thus, the presence of the fixation point reduced the response to the receptive-field stimulus whether or not the cell responded to the fixation point itself.

In the blink plus attention task the suppressive effect of the fixation spot on the response to the receptive-field stimulus was often strikingly demonstrated when the fixation point reappeared while the visual stimulus was still on. Figure 10 shows the effect of the return of the fixation point on the response to the stimulus. Figure 10A shows the response of the stimulus during the blink period. Figure 10B shows the response during the blink plus stimulus attention task as the fixation point reappeared. The response of the cell to the stimulus was suppressed as the fixation point came on again with a regular latency equal to that of the visual response to stimulus onset. While this is a particularly striking instance, the same result was seen in all the neurons; for example, in both Figs. 8 and 9 this effect of the return of the fixation point can be seen in the upper-right panel. The fixation point's suppressive effect on neuronal responses occurred with the same latency as that to a visual stimulus and this similarity of latency suggests that the suppression reflects an interaction within the visual system induced by stimulus. This observation emphasizes the difference between the visual response to the fixation point and the suppressive effect of the fixation point: the fixation point, which is at the most sensitive part of the receptive field, produces either an excitatory response (Fig. 9) or no apparent response (Fig. 10) and also has a

It has been argued that visual spatial attention should meet two criteria: spatial selectivity and response independence (39). Our tasks do use a response (bar release) that is unrelated to the location of the stimulus. We did not, however, test for spatial selectivity.
FIG. 8. Effects of the fixation point and of shift of attention on the response of a cell to the visual stimulus. Tasks in the left column required the monkey to respond neither to the presence of nor to any change in the stimulus but only to the dimming of the fixation point (no stim attention). Tasks in the right column required the monkey to respond to the dimming of the stimulus in order to obtain a reward (stim attention). Tasks in the upper row did not have the fixation point present at the time of onset of the stimulus (no fixation point); tasks in the lower row did (fixation point). Only trials in which the monkey made a correct response are included. The strongest response to the cell is in the upper left raster where there is no fixation point and no attention to the stimulus; the weakest response is in the lower right where there is both a fixation point and attention.

Suppressive effect on the unit's response to another stimulus.

For the cells illustrated in Figs. 8 and 9, the response in the paradigm with no fixation point and no attention (upper left) was significantly better than the response in the paradigm with both factors present (lower right). For the 32 cells on which we made a statistical comparison, 30 cells showed such a significant difference, $P < 0.05$ (for 26 cells, $P$
effect due to attention to the stimulus was less than that due to the presence of the fixation point. In only two cells was the order

\[ \text{CONTRA} \quad \text{IPS} \]

\[ \text{no stim attention} \quad \text{stim attention} \]

\[ \text{no fixation point} \]

\[ \text{fixation point} \]

\[ \text{CO54} \quad 200 \text{ MS} \]

**FIG. 9.** Effect of the fixation point and attention to the stimulus on a cell with a visual response to the fixation point (seen in the upper left panel when the fixation point reappears). The organization of this figure is similar to that of Fig. 8. Again, the response is strongest in the upper left (no fixation point and no attention) and weakest in the lower right (fixation point plus attention).

< 0.005, including those in Figs. 8 and 9). The responses to the receptive-field stimulus in the other two behavioral tasks (e.g., upper right and lower left in Figs. 8 and 9) were intermediate in strength. For 30 of the 32 cells these response strengths were ordered with stimulus-evoked responses in the blink plus stimulus attention task second and the fixation task with no attention third (as in Figs. 8 and 9), indicating that the suppressive

\[ \text{A} \quad \text{F} \]

\[ \text{S} \]

\[ 2^\circ \]

**FIG. 10.** Effect of the fixation point on the response to the stimulus. A: response of the cell to the stimulus in the blink task. B: effect of the reappearance of the fixation point on the stimulus presented in the blink task. In B, the raster and histogram alignment is at the return of the fixation point in the blink plus attention task. The return of the fixation point caused a brief decrease in the cell’s response to the stimulus.

\[ \text{BZ44} \quad 200 \text{ MS} \]
of response strengths in these middle two conditions reversed. 

These experiments show that attention to a stimulus by the monkey under our conditions not only fails to increase the response of the cell to that stimulus but actually decreases it. Therefore, it seems unlikely that the increased response to the stimulus during the original blink task is related to a shift of attention from the fixation point to the stimulus; rather, the improved response occurs because the fixation point is absent during stimulus presentation and, therefore, does not exert its suppressive influence on the stimulus.

Receptive-field size

Since during the blink of the fixation point cells responded to peripheral stimuli that were ineffective while the fixation point was present,
the sensitivity of the cells to such peripheral stimuli must be increased in the blink condition. This suggests that receptive-field sizes should appear larger during the blink, and they do. For example, for the cell shown in Fig. 11, there was a response when the monkey was fixating and the stimulus was superimposed on the fixation point (condition B on the top row), and there was a response during the blink of the fixation point (condition B on the bottom row). In the distant contralateral visual field (Fig. 11, left) and in the ipsilateral visual field (Fig. 11, right), the cell gave no discernible response to the stimulus during the fixation task, but it responded well during the blink task. Figure 11 shows that the location of the stimulus can be chosen so that there is no response to the stimulus when it is presented during the fixation task, while there is a clear response to it when it is presented during the blink task. Changes in the sensitivity of the cell to visual stimulation lead to apparent changes in visual receptive-field size; the field is relatively constricted with the fixation point on and expanded with the fixation point blinked off. We found this change in the receptive-field size in 32 of the 36 cells in which receptive-field size was completely determined in both fixation and blink tasks.

The sizes of the receptive field during combinations of fixation, blink, and attention tasks are shown in Fig. 12. The points representing cell discharge to stimulus onset at 10° from the fovea in the contralateral visual field would indicate a response during the blink task but no response during the fixation plus stimulus attention task. The edge of the receptive field has not yet been reached in the former task, but in the latter task the edge of the receptive field has been reached or passed. The tasks in which an intermediate field size is obtained are those in which only one or the other of the suppressive influences, fixation point or attention, are present.

Cell responses in anesthetized, paralyzed monkey

The TE region of inferior temporal cortex is large and might well consist of multiple regions. Desimone and Gross (6) reported that cells within area TE with a given receptive-field size were clustered together and different areas might have cells with different receptive-field sizes, raising the possibility that the cells we studied were drawn from a different or a very limited part of the population studied previously in the anesthetized, paralyzed monkey. We therefore performed several experiments on anesthetized, paralyzed monkeys using methods similar to those used routinely in Gross’s laboratory (6). We recorded from two of the monkeys we had used in the awake state, using the same cylinder, same microelectrodes, and the same depth of recording as we had used when the monkeys were awake.

Of 45 cells studied in four penetrations through the inferior temporal cortex, 82% responded to our visual stimuli. Although we did not study those cells intensively, we found many cells responded more vigorously to brushes than they did to spots of light and that these complex stimuli produced the most vigorous response in the central part of the visual field. As indicated in Fig. 13 (cell P16), the size of the receptive field was sometimes larger when mapped with a brush than when mapped with a spot. Indeed, some cells re-
Three major points emerge from these experiments on single cells of inferior temporal cortex in awake, trained rhesus monkeys. First, when the monkey fixates on a spot of light, the response to the receptive-field stimulus is weaker and the area of the visual field over which the neuron responds to the stimulus is more limited than when it fixates in the absence of such a spot. Second, if the fixation task is modified so that the monkey is required to attend to a receptive-field stimulus in order to respond to a dimming of it, the response to the stimulus is weakened and the area of the visual field is constricted. These two effects—the presence of the fixation point and attention to the stimulus—are additive, so that the size of the response of a cell to the stimulus is smallest when both influences are present and largest when neither influence is present. Third, when studied in the absence of the fixation point and attentional influences, the receptive fields of inferior temporal neurons are found to be most sensitive close to the fovea, to be large, and to extend into the ipsilateral visual field, as in the anesthetized, paralyzed monkey (6, 14). We will discuss each of these points—visual interaction, effect of attention, and receptive-field characteristics.

**Visual interaction**

Fixation on a visual target suppressed the neuronal response to the receptive-field stimulus. Our hypothesis is that this suppression is a result of an interaction between two stimuli within the visual receptive field of a cell. Suppression was observed only when a visual stimulus, the fixation point, was present on the fovea. In addition, we were able to show that the suppressive effect of the fixation point on the visual response to the stimulus occurred with a latency appropriate for a visual response. We have not explored the physiological basis for this suppression, but the presentation of a second receptive-field stimulus at selected points within the visual field during the blink of the fixation point should reveal the parameters of the visual interaction. Such a visual interaction seems more likely than another explanation, a shift of attention to the stimulus as the fixation point goes off. To explain our results, a shift
of attention should lead to an increased neural response to the stimulus, but such a shift in our task actually led to a decrease in the response of the cells to the stimulus.

Such suppressive effects of a stimulus at one location in the visual field on the response to a stimulus at another location in the visual field are not at all unique; similar effects occur at many points in the visual pathways. For example, in the retina (9, 20) and the lateral geniculate nucleus (2, 8), such a suppressive effect is referred to as the shift or periphery effect in which movement of a stimulus far outside of the excitatory receptive field of a cell frequently reduces the response to a visual stimulus within the excitatory area. In the superior colliculus, a stimulus placed outside of the excitatory receptive field of a cell has a suppressive effect on the response to a stimulus falling within the excitatory region (33, 40). Changes in response due to stimulus interaction when both stimuli are within the excitatory region of the visual field have been observed in the lateral geniculate nucleus (4), the striate cortex (18), and the superior colliculus (33, 40). Unfortunately, we do not know enough about the parameters of the interaction between stimuli in the inferior temporal cortex to make direct comparisons to these visual interactions occurring at earlier steps in the visual pathway.

One effect of the visual interaction, regardless of its mechanism, is to constrain the region of the visual field over which a stimulus produces a response in an inferior temporal neuron. While we have observed this effect in an artificial laboratory situation, we think it is a mistake to dismiss it as a laboratory artifact. Gaze is frequently directed to particular features of visual objects. Fixation of these features places a "stimulus" on the fovea, and this stimulus on the fovea should make inferior temporal neurons less responsive to other objects. We do not know whether this constriction of the receptive field at a neuronal level has any correlate at a perceptual level. But a plausible correlate is found in the demonstrations that the size of the visual field over which a visual discrimination can be made, the functional visual field, can be altered. For example, the visual thresholds for detecting letters in the periphery increased when subjects were also required to detect the offset of a fixation point that was moving (1, 37). Similarly, a central fixation task constrained the region of the visual field in which a particular form could be detected in a background of other forms (16). These experiments show that the size of the functional visual field can change for perception in humans much as the effective size of the visual receptive fields can change for inferior temporal neurons in the monkey, though they do not indicate that the phenomena are related.

**Visual attention**

The suppressive effect of attention to the stimulus (within the restrictions already indicated in footnote 1) appears to be paradoxical. In this region of the brain, which has been shown to be so critical for behavioral responses dependent on identifying patterns, our initial guess was that the neural response to the stimulus would be improved when the monkey was required to respond behaviorally to, and of necessity attend to, the stimulus. That guess was wrong. Attention to the stimulus in order to respond to its dimming led to a decreased response. This is in striking contrast to the enhanced response seen under similar conditions in the parietal cortex (5).

The decrease in response is also in contrast to the improved response seen in previous experiments on awake monkeys while the monkeys were performing a visual delayed matching task (10, 13, 21). The difference in modulation is likely to result from differences in the aspect of the stimulus to which the monkeys were required to respond. In our tasks the monkeys detected a dimming of the stimulus—a luminance discrimination. In the other experiments the monkeys made pattern or color discriminations. Recent experiments in our laboratory (27) have used the same basic behavioral tasks as described in this report but have required the monkeys to attend to the shape of the stimulus rather than a luminance change. Under these conditions some inferior temporal cells respond more vigorously than when the monkeys need not respond to the stimulus shape at all. Therefore, these subsequent experiments emphasize that not only is attention important but also the type of attention is important. Until these most recent experiments, the analysis of
changes in cellular activity correlated with attention have been carried out with the stimulus as a target for a saccadic eye movement (39) or with detection of a luminance change in the stimulus, as in the present experiments. What is now emerging from our experiments is the importance of studying attention in a way appropriate to the brain area being investigated.

Our observations on the effect of fixation and attention on the cells in the inferior temporal cortex are very different than the observations made on cells in the parietal lobe. As already noted, the decreased response of temporal lobe neurons when the monkey responds to a dimming of the stimulus is in striking contrast to the enhancement of neauronal response seen in parietal cortex in the same task (5). In addition, Mountcastle, Anderson, and Motter (25) found that attentive fixation (the requirement that the monkey maintain fixed gaze) irrespective of whether the fixation spot was present or absent (as in a blink task) led to an increased response in parietal neurons. These and several other differences between inferior temporal and posterior parietal cortex can be summarized as follows: 1) the sensory aspect of the fixation spot affects inferior temporal neurons, while the maintenance of gaze seems to influence parietal neurons (25); 2) behavioral response to a luminance change causes a decrease in the response of cells to a receptive-field stimulus in inferior temporal neurons, while it causes an increase in the response of parietal neurons (25); 3) the foveal region is almost always within the receptive field and is at the most sensitive part of the receptive field of inferior temporal neurons; the receptive fields of parietal neurons frequently do not include the fovea and virtually always have the most sensitive part of the receptive field some distance away from the fovea (24); 4) while neither inferior temporal cortex nor parietal cortex have a demonstrated retinotopic map, all inferior temporal neurons emphasize the same part of the visual field, the center, while the emphasis of parietal neurons is distributed among different parts of the visual field (24).

The major similarity between these two regions of presumed higher visual function is that the receptive fields are large. These differences in neuronal activity must be correlated with differences in the function of the two areas of neocortex, but at this point the significance of the neuronal differences remains unknown.

Receptive-field organization in awake and anesthetized monkeys

The receptive fields of inferior temporal neurons in the awake monkey in the absence of a fixation point and visual attention are similar to those previously reported in the anesthetized, paralyzed monkey (6, 14). In both the anesthetized monkey and the awake monkey, the most sensitive part of the receptive field is always at or near the fovea, and sensitivity falls off gradually toward the periphery. The receptive fields are large under both conditions, and the receptive fields are primarily to the contralateral visual field with some extension into the ipsilateral visual field. We have confirmed these observations in the awake monkey as well as for a small population of cells in the anesthetized and paralyzed monkey. The extension of the receptive field into the ipsilateral receptive field was more limited in our experiments as compared to cases illustrated by Gross et al. (14). This might have resulted from our sampling cells in clusters whose receptive fields did not extend very far across the midline, a possibility suggested by the wide range of receptive-field crossing observed by Desimone and Gross (6).

Gross et al. (14) and Desimone and Gross (6) also emphasized that some neurons in inferior temporal cortex in the anesthetized, paralyzed monkey gave a substantially stronger response to (or even required) complex visual stimuli such as brushes, hands, and faces, than to the usual spots, bars, and slits used to stimulate single cells in other parts of the visual system, such as striate cortex. Similar results have been reported in awake monkeys (13, 36). We also found a tendency for complex stimuli to be more effective in the anesthetized, paralyzed monkey, but in the awake monkey we did not study the influence of the form of the visual stimulus on neuronal responses. We were able to obtain responses in the vast majority of inferior temporal neurons using spots or slits of light. Because the responses were consistent enough to allow us to examine the influence of the fixation point and of attention on the stimulus-evoked visual responses, we did not attempt to vary the visual properties
of the stimulus further in these experiments. We believe, however, established the behavioral conditions under which a systematic analysis of the visual properties of inferior temporal neurons in the awake monkey can be studied in future experiments.

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REFERENCES


37. Webster, R. G. and Hasselbalch, G. M. Influence on extreme peripheral vision of attention to a visual or auditory task. J. Exp. Psychol. 68: 269–272, 1964.

