

Visual Receptive Fields of Striate Cortex Neurons in Awake Monkeys

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THE EXPERIMENTS of Lettvin and colleagues (25) and Hubel and Wiesel (19) have indicated that a neuron in the vertebrate visual system is sensitive to particular characteristics of the visual stimulus. These characteristics have been referred to as the "trigger features" of the stimulus (3) and include such factors as size, shape, orientation, color, and rate and direction of movement; the area of the visual field over which the stimulus is effective is referred to as the receptive field of the neuron (17). Receptive-field characteristics of visual system neurons have subsequently been determined in a wide range of animals (for references see 7, 16). In addition, Hubel and Wiesel (19-24, 30) have shown that there are changes in the characteristics of the stimulus needed to activate a neuron at successively higher levels of the visual system. In both cats and monkeys they observed a progressive change in the predominant type of receptive field from the circular receptive fields of retinal ganglion and lateral geniculate cells, through the elongated receptive fields of the simplest cortical cells, to the more complex fields of other cortical neurons.

This understanding of the visual system has been derived entirely from experiments in which the animal was paralyzed and frequently also anesthetized. Such procedures have been designed to eliminate all eye movements, particularly the small eye movements of physiological nystagmus that are characteristic of normal vision (1). The purpose of the present experiments was to determine whether receptive fields of striate cortex neurons in the awake, behaving animal are similar to those in the anesthetized,

paralyzed animal. Large eye movements were successfully eliminated by training monkeys to do a visual fixation task, and receptive-field characteristics were determined during successive short fixation periods. Particular attention was devoted to comparing the effects of stationary and moving stimuli on the responses of the neurons studied.

A preliminary report of these experiments has been presented previously (32).

METHODS

Training procedure

Six monkeys (*Macaca mulatta*) were trained to fix their eyes on a point on a tangent screen 58 cm in front of them. The monkey sat in a primate chair (Fig. 1), and each time it pressed a bar a spot of light appeared as the fixation point. This fixation light remained on for a variable time, between 1 and 3 sec. At the end of that time the light dimmed for about 400 msec, and if during that time the monkey released the bar, it was rewarded with a drop of fruit juice or water. If the monkey released the bar at any other time, the fixation light went off without any reward being given. The principle of this training procedure was to make the fixation light small enough and the dimming period short enough so that any time the monkey looked away from the fixation light there was less chance of seeing the dimming, and therefore less chance of obtaining the reward.

The monkeys reached this end point in their training through a series of steps. First, a large slit of light $2.0 \times 0.3^\circ$ was used as the fixation light, and the stimulus change was a tilting of this slit rather than a dimming. The period before the stimulus change was less than 0.5 sec, and the time allowed for release of the bar was at least 4 sec, so that almost any depression and release of the bar was associated with liquid reward. Then the period before the stim-

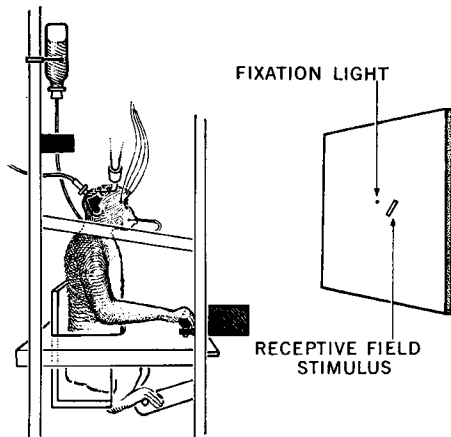


FIG. 1. Schematic drawing of a monkey sitting in the primate chair during an experiment. The monkey was trained to look at a small point, the fixation light, and during this time a search for the receptive field of a striate cortex neuron was made with a second stimulus, the receptive-field stimulus. Correct manipulation of bar in front of the monkey produced a drop of liquid reward from the tube which was in front of the monkey's mouth well below its line of vision. Skin electrodes were attached around the eyes to record electrooculograms, the head was held by two restraining bars, one on each side of the head (only one bar is illustrated), and a microelectrode advancer was attached to a base implanted on occipital bone.

ulus change was gradually lengthened to 3 sec, and finally the duration of this period was varied randomly. The time allowed for release of the bar was reduced to 1 sec. The monkey had to wait longer for the stimulus change and respond faster after it occurred. Next, the size of the stimulus was reduced in several steps to $0.3 \times 0.07^\circ$, and the stimulus, instead of tilting, dimmed. The degree of difficulty of the task, and consequently the quality of the fixation, could be increased at the end of this training procedure and throughout the experiment by changing three parameters: by reducing the fixation light to a spot as small as 0.07° in diameter, by decreasing the amount by which it dimmed, and by shortening the time allowed for release of the bar.

Monkeys were given access to the training apparatus for about 4 hr/day, 5 days/week, for several months. Most of the training was done while the monkey was loose in a transport cage with only final training being done after the monkey was in the primate chair. Particularly astute monkeys learned the task within 3 weeks, but overtraining was always done to assure more reliable performance. A few monkeys

were unable to learn the task within several weeks, and these were rejected.

During this training procedure, whether or not the monkey was fixating was inferred from comparison of the number of times the monkey pressed the bar to start the fixation period with the number of times it correctly released the bar. To verify that fixation was occurring, eye movements were measured using electrooculograms while the monkey sat in the primate chair with its head held rigidly (according to the method devised by Everts, 12). Under sodium pentobarbital anesthesia, four bolts were implanted in the skull, and after recovery from surgery these bolts were connected to two restraining arms secured to the primate chair, as illustrated in Fig. 1. Silver chloride electrodes (Beckman miniature biopotential) were attached to the skin at the outer canthi of the eyes for recording in the horizontal plane, and above and below one eye for recording in the vertical plane. A sample of the horizontal oculograms is shown in Fig. 2A. The eye movements were greatly reduced during the fixation periods indicated by the dark bars in the upper record of Fig. 2A. The size of the residual eye movements is indicated by the lower record of Fig. 2A. Here the monkey followed a movement and return of the fixation point through 3° of arc. The amplitude of the deflection is clearly discriminable above the background noise level. Similar records were obtained for the vertical oculogram except that a 4° movement was usually the smallest reliably detectable eye movement. A sample of several fixations showing the eye movement recorded in both the horizontal and vertical planes is shown in Fig. 2B. Any eye movement smaller than a few degrees was difficult to distinguish from the background noise, and therefore the small drifts and flicks of physiological nystagmus could not be detected. However, any movement larger than several degrees was clearly visible and fixation periods during which such larger movements occurred could be rejected.

For up to 4 weeks following implantation of the restraining bolts, the monkey was given further training in the fixation task under conditions identical to those to be used in the subsequent recording sessions, including head restraint and attachment of oculogram electrodes. The sequence of events during this final training and during the later recording sessions is illustrated in the lower two traces of Fig. 2B. Successive upward deflections of the line labeled "fixation light" indicate depression of the bar, onset of the fixation light, dimming of the light, and presentation of reward when the bar was released in time. A second stimulus, the

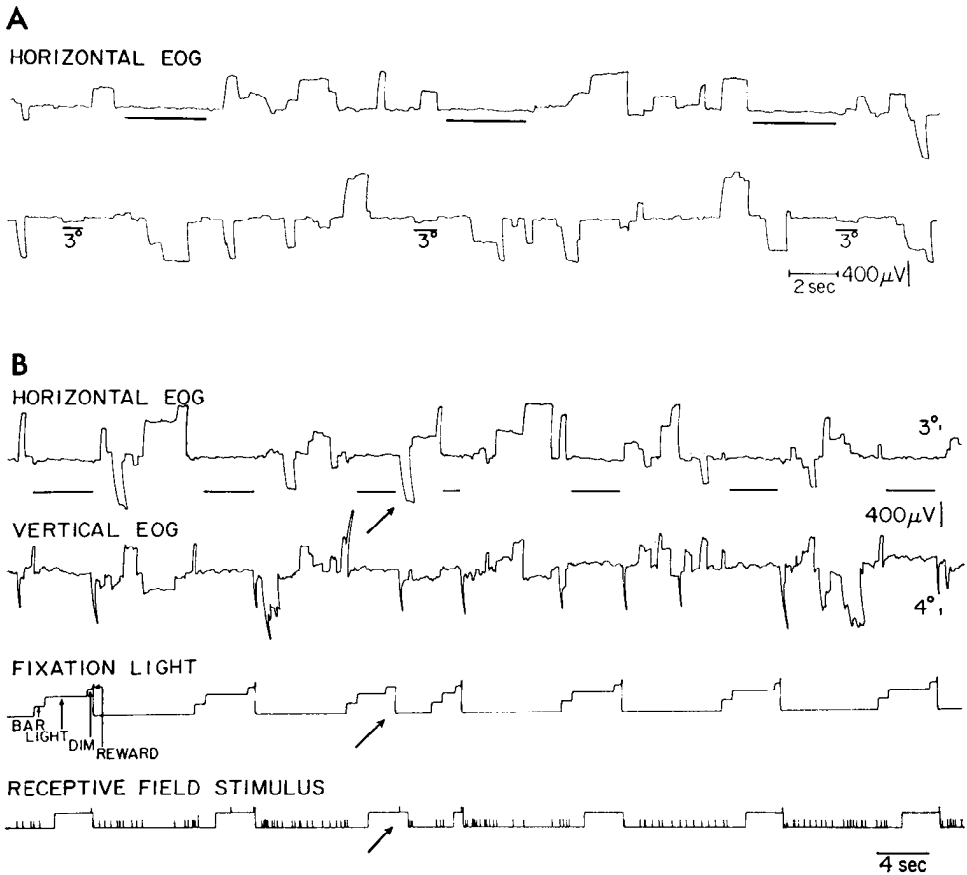


FIG. 2. Eye movements and stimulus events. *A*: electrooculogram (EOG) of horizontal eye movements. Upper trace shows reduction of eye movements during the fixations indicated by dark bars. Lower trace shows amplitude of deflection with 3° eye movements. *B*: simultaneous electrooculograms of eye movement in horizontal and vertical planes. Fixations are indicated by dark bars between the top two traces; amplitude of eye movements is indicated by the short vertical calibration lines on right: 3° for the horizontal EOG and 4° for vertical EOG. Lower two lines indicate events associated with fixation light and receptive-field stimulus. Short vertical lines on the receptive-field indicator show when an eye movement greater than 3° in the horizontal or 4° in the vertical direction occurred. Arrows point to a horizontal eye movement away from the fixation point during a fixation period.

receptive-field stimulus, is indicated on the next line (and in Fig. 1); this stimulus was used during the later recording sessions to determine the type of light stimulus necessary to affect a particular unit. The fixation light did not come on until 0.5 sec after the bar was depressed, and the receptive-field stimulus did not come on until 1.0 sec after the bar was depressed. The separation of these events in time permitted identification of unit responses associated with either the act of pressing the bar or the onset of the fixation light; no striate cortex units studied were associated with either of these events. It was frequently useful to have an interval between successive fixations, as in Fig. 2, and this was obtained by automatically disconnecting the bar for a period of seconds

after each release of the bar. Deactivation of the bar was indicated to the monkey either by a series of clicks or by covering the fixation light. Schmitt triggers were set to give a pulse each time an eye movement larger than 3° in the horizontal direction or 4° in the vertical direction occurred, and these pulses are shown along with the receptive-field stimulus indicator in the bottom line of Fig. 2*B*. Large eye movements during the time the receptive-field stimulus was on were thus clearly indicated, permitting easy identification of poor fixation periods. These pulses were not used for controlling the liquid reward except for final training in a few cases. Note that the fixation period indicated by the arrows was interrupted by a large horizontal eye movement away from the

fixation point; no reward was given, and the movement was indicated by a pulse on the Schmitt trigger channel.

Recording procedure

Following this final training, the monkey was anesthetized, a 10 mm trephine opening was made over the striate cortex, and a stainless steel cylinder was implanted with the dura left intact. This implanted cylinder and the microelectrode advancer that was attached to it during the recording sessions were the same as those developed by Evarts (11, 13). Recording sessions began several days after recovery from surgery. Single-cell responses were recorded using glass-insulated platinum microelectrodes (31). When a clearly distinguishable single-cell response was obtained, a search was made for its receptive field by projecting the second stimulus, the receptive-field stimulus, onto the screen in front of the monkey.

The receptive-field stimulus was a white light produced by a projector with a tungsten filament lamp and was 1.0–1.5 log units above the background illumination of 1 cd/m². The stimulus shapes were produced by slides in the projector and the shapes available included circular, rectangular, or triangular spots of light; circular, rectangular, or triangular dark areas with lighter surrounds; straight and curved edges between light and dark areas; stripes of alternate light and dark areas; and an assortment of more complex patterns. The size, orientation, and position of each stimulus could be varied, and movement was produced by moving the projector. Rate of movement was determined by passing the stimulus over two photocells a known distance apart, measuring electronically the interval taken by the stimulus to cross from one photocell to the other, and then calculating the velocity of movement. The receptive-field stimulus was turned on and off during the fixation periods by a card that interrupted the light beam in front of the projector and that was moved by a galvanometer. This mechanism produced nearly silent stimulus control but entailed a long rise and fall time for the stimulus of about 40 msec. Since stimulus presentations of several seconds were always used, and since latency was not measured, this slow rise time was not important in these experiments. The indicator for the receptive-field stimulus in the figures came on when the stimulus change was 70% complete.

The search for the receptive field of the particular unit was made during successive fixation periods: the first step was to locate the area in the visual field where spots or slits of light affected the particular unit. Once found, this

would also be the same area where stimuli would affect all other units in the same penetration and not far from the stimulus area affecting units in adjacent penetrations. Then the size, shape, orientation, and type of stimulus movement which produced the best unit response was worked out on successive presentations. The effectiveness of a stimulus was judged by the change in frequency of unit discharges it produced. The best stimulus was one that produced the greatest change in frequency of unit responses—either up, which will be referred to as an excitatory response, or down, which will be referred to as an inhibitory response. The aim of the search for the receptive field of a unit was to determine the organization or trigger features of the field rather than the fine detail. For example, even when a unit appeared to respond best to a slit of light, a slit longer or wider by a fraction of a degree or slightly curved rather than rectangular might in fact have been the best stimulus. Such differences would not have been detected in the present series of experiments.

The response of the unit was determined during the experiment by listening to the unit discharge on an audio monitor and by looking at oscilloscope traces of unit responses and at penwriter records of pulses triggered by the unit responses. The penwriter also recorded horizontal and vertical eye movements and the other information about the fixation light and the receptive-field stimulus shown in Fig. 2B. The penwriter record permitted direct comparison of unit responses with stimulus events and eye movements. These variables were also recorded on magnetic tape. After the experiments the responses of units were further examined by looking at filmed records, by counting unit activity in certain stimulus periods on an electronic counter, and by producing dot pattern displays of unit responses following successive stimulus events (29).

Each day monkeys would do the fixation task between 1,000 and 2,500 times. To determine the receptive-field characteristics of a particular unit required at least several hundred fixations although adjacent units frequently had very similar receptive fields and required fewer fixations for adequate study. The area of striate cortex exposed by the implanted cylinder was large enough so that on successive days a number of penetrations could be made, and a number of receptive fields could then be studied in the same monkey. Toughening of the dura, which produced breakage of the electrodes, ended recording sessions after 2–4 weeks. The implanted cylinder was then removed under anesthesia and a second cylinder was placed

over the striate cortex of the opposite hemisphere. Recording then resumed for several additional weeks. Alternatively, a larger cylinder (18 mm in diam) was placed over the midline and unit responses were recorded from both hemispheres through the one implanted cylinder.

To identify the approximate locations of the electrode tip, a lesion was made in some penetrations by passing current through the microelectrode. At the end of the experiment the monkey was anesthetized and perfused with saline and then formalin. Frozen or celloidin-embedded sections of striate cortex were stained with cresyl violet.

RESULTS

Receptive fields were determined for 218 units in the striate cortex. The units were spontaneously active although a few had such low levels of spontaneous activity that they were barely detectable before the effective stimulus fell on their receptive fields. The range of spontaneous discharge rates among neurons was between 40 impulses/sec and a few tenths of an impulse/sec. A

full-field pattern of crossed lines was sometimes placed on the screen while the electrode was being advanced, but this was not effective in eliciting responses from any silent units.

All penetrations with the microelectrodes were made in areas close to the midline in area 17. Receptive fields were no closer than 3.5° and seldom farther than 10° from the fixation point so that the fields studied were in areas surrounding the fovea. Fields were in all four visual quadrants but were usually in the lower hemifield.

Receptive-field localization

In the anesthetized, paralyzed animal, the stimulus had to be in a specific part of the visual field to maximally affect the response of a unit in striate cortex (19, 24). In the awake monkey, receptive fields were also localized with discrete central areas. An example of such a receptive field is shown in Fig. 3. The most effective stimulus for this unit was a spot of light $1.5 \times$

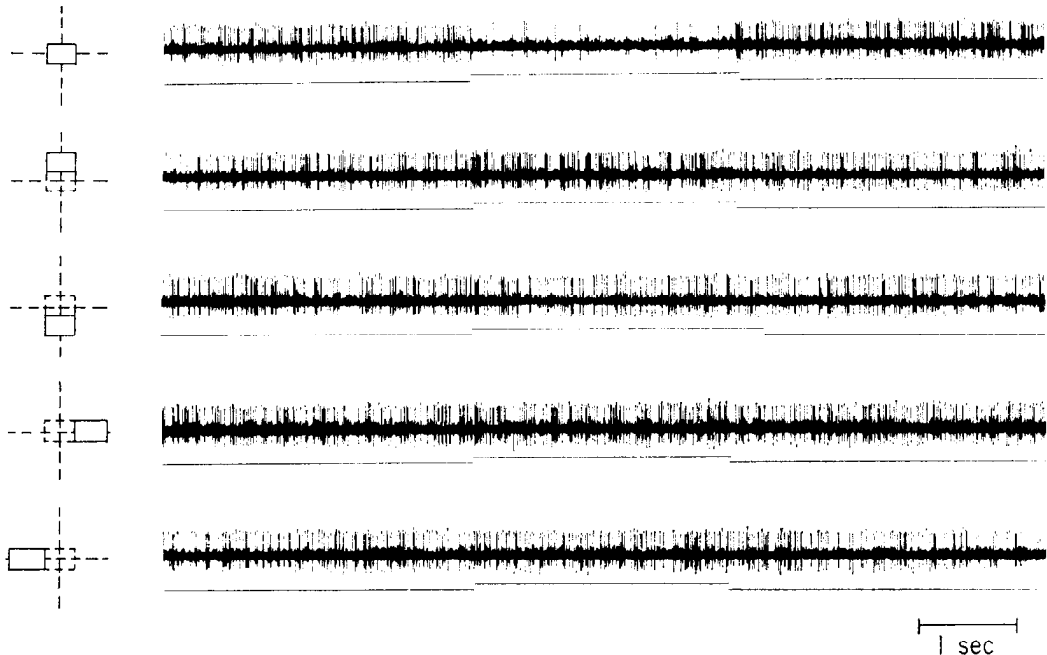


FIG. 3. Response of a unit to a localized spot of light. Upper line of each record shows unit response; an upward deflection of the lower line indicates presence of the stimulus. Position of the spot of light, $1.5 \times 1.0^\circ$, is indicated to the left of each record; receptive field was located about 5° from fixation point. In the top record, the spot of light placed on the receptive-field center inhibits unit activity. In succeeding records, the spot of light is placed above, below, to right, and to left of the receptive-field center and has little effect on unit activity.

1° located about 5° from the fixation point. At the most effective point (Fig. 3, top record) the stimulus inhibited the unit activity. When the same spot of light was placed above, below, or to either side of the most effective point, little or no effect on the unit response was observed.

For the striate cortex units with the simplest receptive fields (including, in the monkey, both those with simple receptive fields and those with circular receptive fields), Hubel and Wiesel identified both a central area and a surrounding or adjacent antagonistic area (19, 24). Although it was possible in the awake animal to determine that the central area of the receptive field was localized, the presence and extent of surrounding or adjacent antagonistic areas was much more poorly defined. For example, when for the same inhibitory-center unit (Fig. 4) the surrounding area was illuminated while only the background light fell on the field center (Fig. 4, middle record), there was an excitatory response. Although this response was barely detectable, it was one of the clearest of such responses observed in these studies; failure to obtain a response with illumination of the surround alone was common. An antagonistic area must have been present even when not detected by this method since in all cases covering both the center and

the surrounding area with light produced a response different from illumination of the center alone. This is illustrated in the bottom record of Fig. 4; diffuse light on both center and surround produced an inhibition of unit activity not nearly so great as illumination of the center alone. For most units diffuse light on both center and surround produced little if any change in rate of spontaneous firing of the unit. The presence of an adjacent or surrounding antagonistic area was investigated for each receptive field primarily by noting the effect of diffuse light, but the size and shape of such an area was not determined.

Shape, size, and orientation specificity

As was the case in the anesthetized, paralyzed animal (19, 24), the most effective stimulus for many of the striate cortex units in the awake monkey was an elongated slit of light; the size and orientation of the slit was critical. For the unit in Fig. 5 the most effective stimulus was a rectangular spot of light $2.1 \times 0.4^\circ$ located about 5° from the fixation point. In all orientations the center of the slit was on the center of the receptive field. The stimulus had its maximal effect on the response of the unit when it was oriented as shown in the third record from the top, it had some effect when oriented as in the fourth record, but

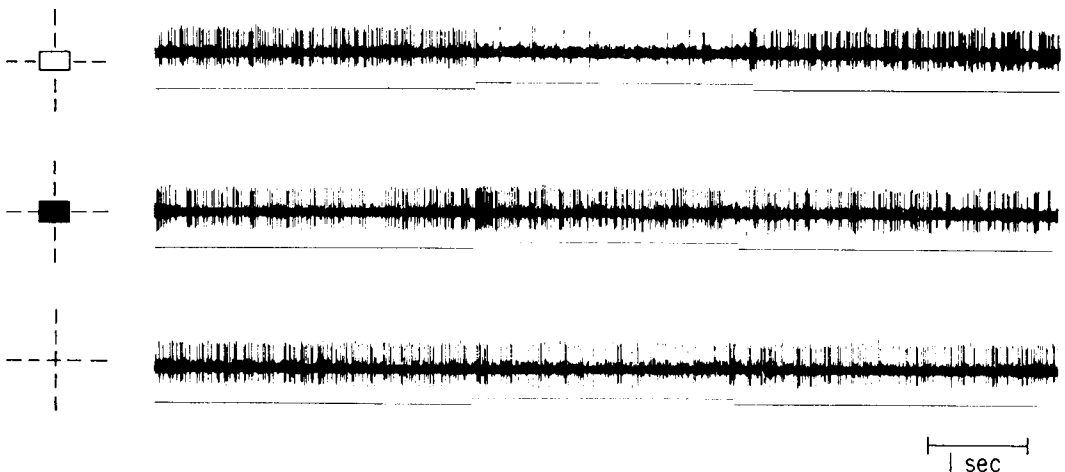


FIG. 4. Effect of surround area of receptive field on unit response. Same unit as in Fig. 3. In upper record, spot of light on the center of the receptive field inhibits unit activity. In middle record, the surrounding area is illuminated in a circular area 8° in diameter and background illumination falls on center of the field; there is little response. In lower record, both center and surround are illuminated in the 8° area and there is only a slight inhibitory response.

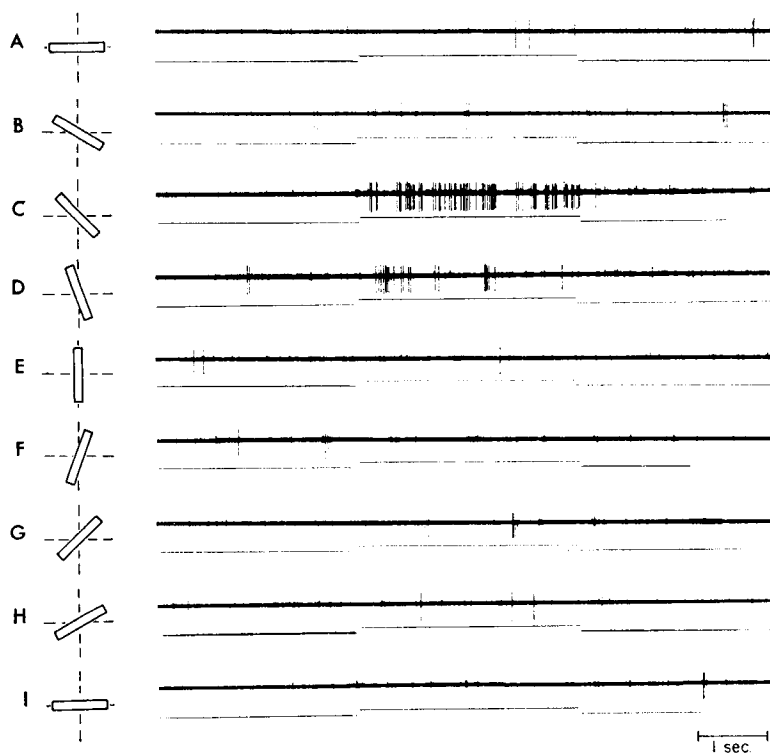


FIG. 5. Response of a single unit to a slit of light with differing orientations. Center of the slit fell on center of the receptive field in all positions but produced unit response over only a small part of the total rotation. The slit was 2.1° long and 0.4° wide, and receptive-field center was about 5° from fixation point.

it had no effect in any of the other positions.

The range of sizes found for the receptive-field centers is indicated by the samples in Figs. 3, 5, and 6, with the size in Fig. 5 over the left end of the receptive field, studied was $1.3 \times 0.3^\circ$. Most fields had excitatory centers, as in Figs. 5 and 6, and only a small fraction had inhibitory centers, as in Fig. 3; but this ratio is most likely a result of the comparative ease of finding excitatory-center fields. A few fields had excitatory and inhibitory areas side by side so that an edge between light and dark was the most effective stimulus.

Nonadapting unit responses

Striate cortex units of paralyzed, *cerveau isolé* cats were reported to give only rapidly adapting responses to the onset of a stationary stimulus; stimulus movement was required for a prolonged discharge (8). Most units illustrated by Hubel and Wiesel (19, 22) were also rapidly adapting, but

there were some that continued to respond as long as the stimulus was present. In the awake monkey, units with a largely nonadapting response to a stationary stimulus were common. The response of such a unit is shown in Fig. 6. In successive orientations one end of the slit of light was always over the left end of the receptive field, which is indicated by the vertical dashed line. The orientation of the slit was first ineffective, then effective as the slit covered the receptive field to a greater extent (the three middle records), and then again ineffective. The light was stationary on the screen at all times and yet, oriented effectively, it produced a vigorous unit response. Moving the stimulus did not increase the response of the unit.

The response to the effective stationary stimulus continued for as long as the stimulus was on (Fig. 6, second and third records from the top); the response was largely nonadapting. This type of unit response accurately reflected the presence or absence

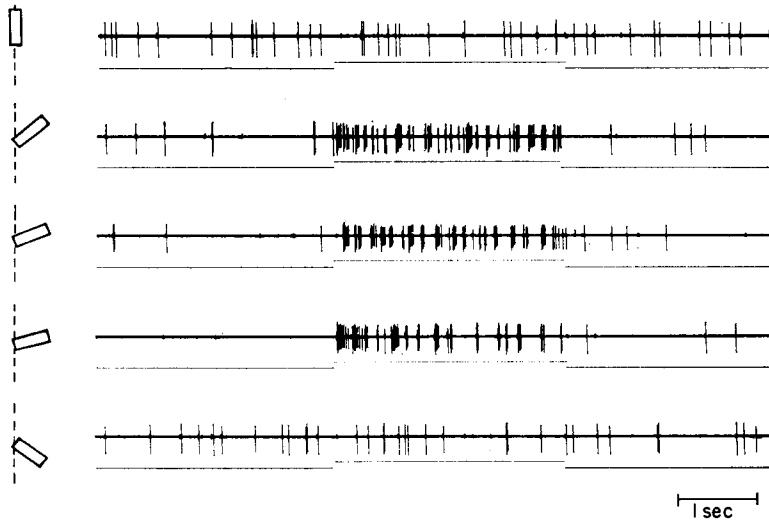


FIG. 6. Nonadapting response of a unit to a stationary stimulus. Slit was $1.8 \times 0.6^\circ$. Dashed vertical line represents position (not extent) of the left end of the receptive field around which the slit was rotated. Slit best covers the receptive field in the second and third orientations illustrated. Left end of the receptive field was located about 9° from fixation point.

of the stimulus in the environment. When the stimulus was not so well centered on the receptive field (Fig. 6, fourth record from the top), more adaptation occurred although still not complete adaptation. In general, there was a tendency for the amount of adaptation to increase as the stimulus was less effectively placed on the receptive field.

Many units responded with a bursting pattern of discharge like that of the unit illustrated in Fig. 6. There was no obvious relation between these bursts and any eye movement large enough to see in the electrooculogram. The bursts were not seen in all units (Fig. 3, for example) although even when no bursting occurred the pattern of discharge was never a regular one with uniform interspike intervals.

In the awake monkeys a vigorous and nonadapting unit response to a stationary stimulus was sometimes accompanied by a depression in the rate of discharge after the stimulus was turned off. Figure 7 illustrates this for the same unit that is shown in Fig. 6. In the upper record the stimulus is in an ineffective position and the rate and pattern of discharge indicate the level of background activity. In the lower record the stimulus is in the most effective position and is presented at intervals of about 4 sec; the activity is concentrated during the stimulus presentation, and the activity between presentations is reduced below the background level.

When the stimulus was moved, many of these nonadapting units did not respond at all, or the response dropped off rapidly

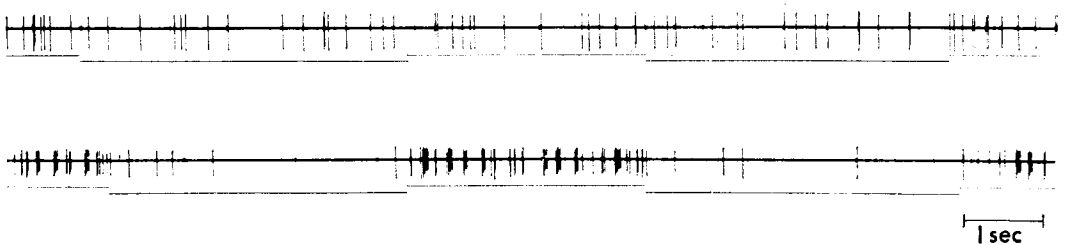


FIG. 7. Depression of discharge rate of a unit following presentation of an effective stimulus. Same unit as in Fig. 6. In upper record, stimulus is in an ineffective position and record indicates spontaneous discharge rate of the unit; in lower record, stimulus is in the maximally effective position and record shows depression of response following end of the stimulus period.

as the rate of stimulus movement increased. Other nonadapting units continued to respond to a moving stimulus but with increasingly shorter durations of response with higher rates of stimulus movement. Some of these units continued to respond to a stimulus moving up to $200^{\circ}/\text{sec}$, and the responses sometimes occurred to even more rapidly moving stimuli (manuscript in preparation). When there was a response to a moving stimulus, it was what would be expected from the receptive-field organization as determined by a stationary stimulus. For example, when a stationary, vertical slit of light was the most effective stimulus for a particular unit, movement of the vertical slit from side to side was also effective, but up-and-down movement of the same slit oriented horizontally was ineffective.

Rapidly adapting unit responses

In the paralyzed, anesthetized cat (19) and in the awake freely moving cat (18), a moving stimulus was reported to be a very effective stimulus for many units. In the awake monkey there were also units which responded best to a moving stimulus, but there was a tendency for units to fall into two groups. In the first group were the units just considered which responded vigorously and with a nonadapting response to a stationary stimulus; some of these units continued to respond to a moving stimulus. A second group of units responded best to a moving stimulus and gave a rapidly adapting response to a stationary stimulus.

An example of a unit response typical of the second group is shown in Fig. 8. A slit of light was moved across the receptive field of the unit at successively higher velocities, as indicated by the numbers (in degrees/sec) to the left of each line. The most vigorous response occurred when stimulus movement was about $8\text{--}12^{\circ}/\text{sec}$. At higher velocities the duration of the burst of response decreased, as did the number of discharges in each burst, until at $240^{\circ}/\text{sec}$ the response was about the same as the response to a stationary stimulus. Units of this type may also continue to respond at higher velocities (manuscript in preparation). At velocities less than about $8^{\circ}/\text{sec}$

the response was less vigorous, and with movement of only $2^{\circ}/\text{sec}$ the response was even less than that to a stationary stimulus (although there were other units in the background which did respond to such a slowly moving stimulus). Each unit of this second group had a limited range of velocities to which it responded best; the velocities covered by this range varied from unit to unit.

Although the best response of the unit

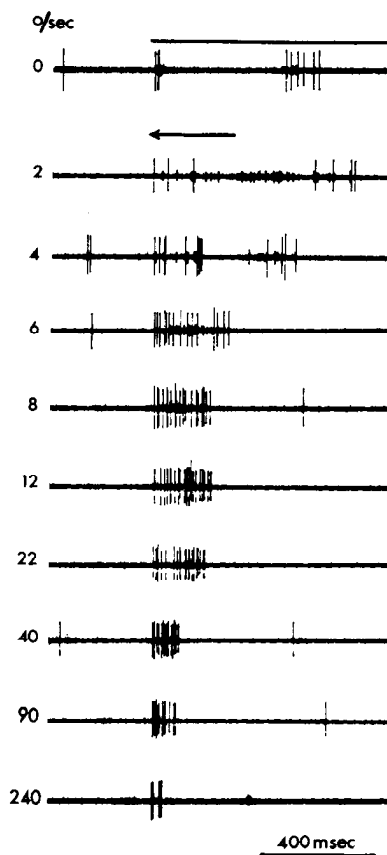


FIG. 8. Unit with best response to a moving stimulus. In top record, a slit of light is stationary on the receptive field during time indicated by line above the unit responses. In second record and in all those below, the same slit of light is moved across receptive field from right to left, crossing the field at about the point indicated by the arrowhead. Rate of movement is indicated next to each record. Receptive field of this unit was 6.5° from fixation point and size of the most effective stimulus was $2.0 \times 0.5^{\circ}$. To measure rate of movement, a slightly longer slit was used which then also passed over photoreceptors adjacent to receptive field and permitted accurate measurement of stimulus velocity.

in Fig. 8 was to a moving stimulus, there was also a brief burst of unit discharges when the stimulus was turned on and not moved (Fig. 8, top record). For this unit the response to a stationary stimulus was poor in comparison with the response to a moving stimulus; some units gave no response at all to a stationary stimulus, others gave a burst of discharge with the onset of a stimulus nearly as vigorous as that to a moving stimulus. The response of these units to a stationary stimulus, however, was always a brief, rapidly adapting response rather than the nonadapting response of the first group of units.

In a series of 50 units in which the response to stimulus movement was studied in detail, 90% of the units could be placed in the two groupings just considered. Units with circular, simple, or complex receptive fields (see last section of RESULTS) had both nonadapting and adapting types of responses. The remaining 10% of the units displayed various combinations of the properties of both the adapting and nonadapting groups. For example, some units were nonadapting to a stationary stimulus but then gave a much more vigorous response to a moving stimulus; other units responded to a moving stimulus with a clear burst of unit discharges and responded to a stationary stimulus with a similar burst, but displayed a nonadapting response for as long as the stimulus was on.

Directional selectivity

In the cat and monkey, directional selectivity is observed for units in striate cortex

(18, 19, 24). Many units in the striate cortex of the awake monkeys also showed such directional selectivity: stimulus movement in one direction produced an excitatory response; movement in the opposite direction produced little or no response or an inhibitory response. The unit shown in Fig. 9 gave a directionally selective response to a moving slit of light about $0.5 \times 1.5^\circ$. Illustrated in Fig. 9 is the unit response during the passing of a series of light and dark stripes that were slightly longer than 1.5° over both the receptive field and an adjacent photocell. With movement from left to right (upper record) there was an excitatory response. Movement of the stripes from right to left (lower record) produced an inhibitory response. The units of small amplitude in the background gave excitatory responses to movement from right to left, indicating that adjacent units have different responses to the same stimulus movement.

What was clear in the awake monkey (but not reported for the paralyzed, anesthetized animal or the awake cat) was that units showing directional selectivity were almost always those of the second group which were rapidly adapting and which responded best to a moving stimulus. The rapidly adapting unit of Fig. 8, for example, showed no response to stimulus movement opposite to the direction illustrated. Not all rapidly adapting units showed directional selectivity.

The nonadapting units of the first group did show some directional sensitivity to stimulus movement (with optimal stimulus



FIG. 9. Directional selectivity. Bottom line in each record is output of a photocell placed just above receptive field. In upper record, a series of slits of light (stripes) is moved at $15^\circ/\text{sec}$ from left to right over receptive field of the unit and the adjacent photocell, producing excitatory response of the unit. In lower record, the same stripes are moved from right to left, producing an inhibition of the unit activity. Receptive field was located 6° from fixation point.

orientation and movement direction) but these differences were slight in comparison with the selectivity of the second group of units. The exception to this association between the rapidly adapting response and the directional selectivity was the category of units with circular receptive fields; these units responded to movement in all directions.

Receptive-field categories

One of the most significant aspects of the work of Hubel and Wiesel (22, 23) is the proposal that the units in visual cortex with different types of receptive fields are sequentially arranged to process visual information. Those units with the simplest receptive fields converge on the next higher level, with a change in stimulus specificity occurring at each level. This inference of a hierarchical arrangement in the cortex was drawn following the observation that units can be placed in categories according to their receptive-field organization. In the awake monkey it was possible to identify units that seemed to fit into similar categories.

The receptive-field organization of the units so far considered (with the possible exception of the unit in Fig. 3) appeared similar to those referred to by Hubel and Wiesel (22) as simple receptive fields. Not all the criteria they used to establish this category were used in these experiments, mainly because of the difficulty of determining antagonistic surrounds. In the present study a receptive field was regarded as simple if it met the following criteria: *a*) the best response of the unit was to an elongated stimulus with a particular orientation in a localized area; *b*) the central area of the receptive field was the same size and shape when small spots of light were used to map the field; and *c*) if an elongated, moving stimulus was effective, it was most effective when the long edge of the stimulus was passed across the long axis of the receptive field.

Receptive fields were obtained which were more complex than the simple receptive fields. These fields were like the simple receptive fields in that units responded best to elongated stimuli of a

particular size, orientation, and direction of movement. But they were considered as more complex because they differed from simpler fields in the following ways: *a*) small spots of light were not effective stimuli for these units, and the spots could not be used to estimate the size of the center of the receptive field; and *b*) the stimulus did not need to be so exactly placed as for the simple receptive fields. An example of such a field is shown in Fig. 10. A horizontal slit of light above an approximately square area 1.5° on each side (indicated by the dashed lines in Fig. 10*A*) had no effect on the response of the unit. When the slit was within the square area (Fig. 10 *B, C, D*), there was a clear, nonadapting response to the stimulus although the response was more vigorous when the slit was placed in the upper parts of the area. A slit just below the area (Fig. 10*E*) produced no response. When a slit of the same size was placed vertically in the field, there was also little response (Fig. 10 *F, G*). Finally, when the whole square area was covered by light, there was no response (Fig. 10*H*), an effect which would not be expected if the horizontal slits within the square area were merely falling in synergistic areas of a simple receptive field. Small spots of light were ineffective stimuli for this unit. Increasing the length of the effectively placed horizontal slits of light did not seem to alter the response significantly; there was no stopped-end effect, as would be expected if the receptive field were similar to those referred to as hypercomplex by Hubel and Wiesel (23, 24). However, since the effect of stimulus length was not checked on all units with complex fields, it would be more accurate to say that this category of complex fields in the present experiments included all units with receptive fields more complex than simple receptive fields.

A few units were stimulated as effectively by a circular spot of light as by a slit of light. The slit was effective in any orientation, and moving the slit across the field from any direction was equally effective. These circular fields have been previously reported for units recorded in striate cortex of the monkey (24) and the cat (6). In the present experiments, whether these responses were from fibers afferent to the

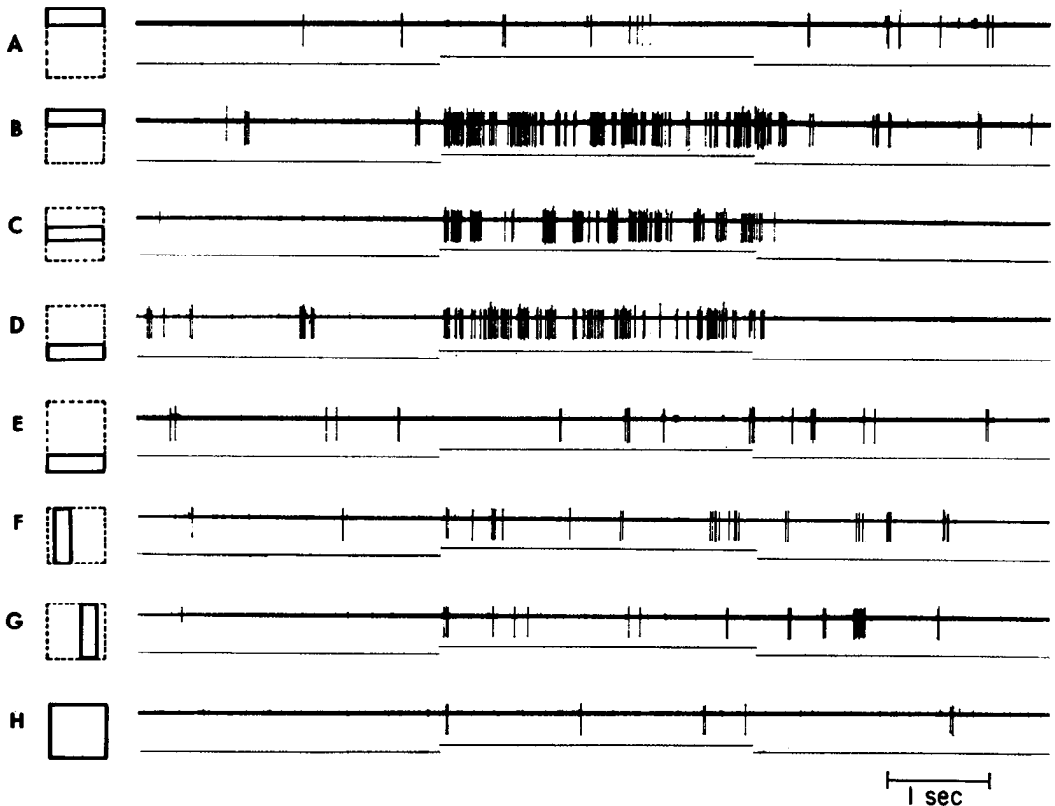


FIG. 10. Response of a unit with complex receptive-field organization. Effective stimulus was a horizontal slit of light $1.5 \times 0.5^\circ$ placed anywhere in the square area (*B, C, D*) indicated by dashed lines. The area was 5.5° from fixation point. Horizontal slits of light above or below the square area (*A* and *E*), vertical slit in the area (*F* and *G*), or illumination of the whole field (*H*) were ineffective stimuli.

cortex or from cortical cells was not determined.

For 169 units enough information was obtained about the receptive fields to characterize them as circular, simple, or complex. Receptive fields were circular for 13% of the units, simple for 60%, and more complex for 13%. The remaining 14% of the units had either simple or complex receptive fields, but the fields were not adequately determined to place in one category or the other. The total of 169 included units responding best to a stationary stimulus and units responding best to a moving stimulus.

In the striate cortex of the monkey, Hubel and Wiesel (24) found that units of similar receptive-field complexity predominated within a particular horizontal level. Units with complex and hypercomplex receptive fields were in upper cortical

layers (II, upper III), units with simple receptive fields were below (lower III, IV), and units with complex and hypercomplex receptive fields were seen again at deeper levels (V, VI). In the present experiments on awake monkeys it was rarely possible to determine the receptive fields of units encountered in roughly the upper half of a penetration through the striate cortex and, beyond initial experiments, little effort was devoted to finding the receptive fields of these units. Presumably, many of these receptive fields were of the hypercomplex variety. In sharp contrast to this, receptive fields of units deeper in the cortex were nearly always determined. The amplitude of the unit responses studied was usually between $100\text{--}300 \mu\text{v}$, but units with spikes as small as $50 \mu\text{v}$ or as large as $600 \mu\text{v}$ were occasionally studied. Most of the units in the lower part of the cortex were dif-

difficult to isolate, particularly when an effective stimulus for a unit was found, since the same stimulus usually also activated units in the background. The small size of the spikes and the difficulty in isolation suggest that the units deeper in the cortex represented activity of small cells.

In a few penetrations a lesion was made to help identify the level in cortex where the response of a particular unit was recorded. The lesions confirmed that the units with determinable receptive fields had been recorded from striate cortex and primarily from the lower layers of cortex, about at the level of layer IV or below.

DISCUSSION

Receptive fields in awake monkeys

The neurons of striate cortex in the awake monkey respond best to patterned light stimulation. Receptive fields of these neurons are well localized; diffuse light is never so effective as a small spot of light. The maximum response of a neuron is obtained when a light stimulus of a specific size and shape is oriented in a particular way. Some neurons respond best to a moving stimulus and show a sensitivity for direction of movement, others respond best to a stationary stimulus. Visual cortical neurons can be classified according to certain features of their receptive fields (22), and fields with circular, simple, and complex organization have been found. Neurons with hypercomplex receptive fields (23, 24) or specific color sensitivity (24) have not been studied.

From the present experiments it is concluded that the basic organization of the simpler types of receptive fields of striate cortex neurons reported for the paralyzed and anesthetized cat (19, 22) and monkey (24) is found also in the awake monkey. It follows that this organization cannot be a result of anesthesia which in some way alters the responsiveness of the neurons (28), although modifications in the response of a particular unit between the awake and the paralyzed, anesthetized state have not been studied.

On the other hand, it cannot be concluded that receptive fields in awake and paralyzed, anesthetized animals are identi-

cal. Factors such as attention, which might be expected to produce differences in unit responses between awake and paralyzed, anesthetized animals were minimized in the way these experiments were done. First, the awake monkey was adapted to the receptive-field stimulus by being exposed to it thousands of times during the training periods. Second, the possibility of reward was always signaled by the fixation light, never by the receptive-field stimulus. Finally, the monkey was required to respond only to the fixation light, never to the receptive-field stimulus. There is no reason to believe that the monkey paid attention to the light which was activating the cells under study. In this light the general similarity between the findings on the awake monkey and the paralyzed, anesthetized cat and monkey is not surprising.

Response adaptation and stimulus movement

In the awake animal the coupling of the response to movement and the adaptation characteristics of the units is particularly striking. Most units (but not all) fall into one or the other of two groups. One group of units gives a vigorous and largely nonadapting response to a stationary stimulus. The nonadapting response is occasionally so vigorous that it depresses the unit activity for seconds after the stimulus presentation, and with periodic stimulation every several seconds the stimulus comes to control the neuron response after as well as during stimulus presentations. For these nonadapting units no movement of the stimulus is necessary to produce a continuing discharge; movement does not improve the response, although many units did continue to respond to a moving stimulus. In contrast to these nonadapting units, a second group is rapidly adapting, and although many of these respond to a stationary stimulus, it is only with a brief burst of discharges. These units respond most vigorously to a moving stimulus and are primarily the ones that show directional sensitivity. No tendency was apparent for either group of units, adapting or nonadapting, to be associated with a particular receptive-field organization, circular, simple, or complex. Although both the non-

adapting and the rapidly adapting types of cortical neurons have been observed in paralyzed, anesthetized animals (19, 22), the tendency for adaptation to be associated with response to movement has not been noted. In the awake animal this relationship between adaptation and response to movement is more readily apparent than the organizational complexity of the receptive field, and this relationship appears to be independent of the organizational complexity dimension.

Directionally selective units (to use the definition of Barlow and Levick, 4) are those that give an excitatory response to movement in one direction and little or no response to movement in the opposite direction. Cortical units that show directional selectivity are found in paralyzed cats (5, 9, 19, 22, 26), monkeys (24), and rabbits (2), and in awake, unrestrained cats (18). In the awake monkey the nonadapting neurons generally show only small differences in response to stimulus movement in opposite directions. These differences could result from a summation over asymmetric excitatory and inhibitory areas of the receptive field, as suggested previously by Hubel and Wiesel (22). But the clearest directional selectivity in the awake monkey is generally shown by units that are rapidly adapting and that respond best to movement. The mechanism of this selectivity has not been determined but there was no indication that an asymmetric receptive-field organization could explain the directional effect. In this respect these directionally selective neurons appear to be more like those in the retina of the rabbit (3, 4). In a recent study of striate cortex neurons in the cat (26), the arrangement of excitatory and inhibitory regions of the receptive field was also regarded as inadequate to explain the directional selectivity observed.

Role of small eye movements

Receptive fields in these experiments were studied while the monkey's eyes were making the fine movements of physiological nystagmus. These eye movements in man (as summarized by Alpern, 1) consist of slow drifts with an approximate size of 5 min of arc and rapid flicks of the eye of about the same magnitude as the drifts. The flicks occur at irregular intervals,

roughly, about 1/sec. Superimposed on these two movements is a small oscillation or tremor with a frequency of 30–80 cycles/sec and a median amplitude of about 17 sec of arc. Although the small eye movements were not measured in monkeys, in light of other similarities between eye movements in monkey and man (14, 15), it is reasonable to assume that the small eye movements are comparable. These small eye movements are always present during normal vision and are necessary for normal perception. If they are eliminated by stabilizing the retinal image (10, 27, 33), clear vision of an object fades within several seconds. The object returns to view when it is moved or otherwise altered.

What effect do these small eye movements have on the responses of striate cortex neurons? Small eye movements could conceivably interfere with detection by the unit of stimulus movement. This is not the case, since there is a type of unit that responds best to a moving stimulus, frequently to a stimulus moving in a particular direction, in spite of the background of eye movements. It seems likely that the eye movements are too small in relation to receptive-field size to produce any effect that could be confused with the larger stimulus movements. This may not be the case, however, when the size of stimulus movements and eye movements are more nearly the same, such as might be the case for small stimulus movements or for small receptive fields in the fovea.

Another possible effect of small eye movements on striate cortex neurons is to shift the stimulus on and off the receptive field. These movements back and forth have been suggested as a mechanism for maintaining the discharge of the visual system neurons in the presence of a stationary stimulus and thereby for maintaining the perception (8). Thus, if there were no eye movement, there should be rapid adaptation of the unit response just as there is rapid adaptation of the perception. Burns, Heron, and Pritchard (8) studied striate cortex neurons in paralyzed but not anesthetized cats and obtained just such rapid adaptation in the absence of small eye movements. A stationary edge between light and dark produced only a brief burst of unit discharge; to obtain a longer lasting discharge it was neces-

sary to move the same stimulus back and forth over the field at about 2–4 cycles/sec.

Since there are always eye movements in awake animals which might move the stimulus on and off the receptive field, one would expect to find only the nonadapting type of unit response. The nonadapting response is observed, but in addition a rapidly adapting type of unit response is also found, even in the presence of small eye movements. The two different types of unit response, therefore, must be related to differences in receptive-field organization or in the response of the units to movement rather than to the presence or absence of eye movements alone. In addition, if the nonadapting response were dependent on the small eye movements, one would expect to see only rapidly adapting responses in the paralyzed animal. Nonadapting responses to stationary stimuli are seen (19, 22), and these presumably have been recorded from foveal as well as extrafoveal units. Both because adapting and nonadapting units are found in the presence of eye movements in the awake animal, and because nonadapting units are found in the absence of eye movements in the paralyzed animal, it does not seem likely that eye movements alone are the mechanism for maintaining unit discharge. Instead, eye movements may produce a more subtle change in a unit response such as a quantitative shift toward a more nonadapting response. Verification of this would require more direct comparison of single-unit response characteristics between normal and paralyzed animals.

SUMMARY

Monkeys were trained to fix their eyes on a point of light on a screen in front

of them for several seconds. Their heads were held steady, eye movements were monitored with electrooculograms, and single-unit responses were recorded from striate cortex. A second spot of white light was used to search for the receptive field of the isolated single unit during successive, several-second periods of fixation. Units studied had receptive fields outside the fovea but seldom more than 10° away from the fixation point, were in roughly the lower half of the cortical depth, and were spontaneously active.

Receptive fields were localized, diffuse light was never so effective as a spot of light, and the most effective stimulus shape was usually a slit of light oriented a particular way. Units could be categorized by their receptive-field organization: circular, simple, or complex. It was concluded that the basic organization of the simpler types of receptive fields of striate cortex neurons in the awake monkey is similar to that in paralyzed, anesthetized cats and monkeys.

Many units gave a largely nonadapting response to a stationary stimulus. Movement of the stimulus was not necessary to maintain a continuous discharge although some of these units responded during stimulus movement. It is unlikely that small eye movements alone are responsible for the nonadapting response of these units although they may contribute to it. In contrast to these nonadapting units, others were rapidly adapting and responded most vigorously to a moving stimulus. It was primarily these rapidly adapting units that showed directional selectivity. These adaptation characteristics appeared to be independent of the organizational complexity of the receptive field.

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