Response of Striate Cortex Neurons to Stimuli During Rapid Eye Movements in the Monkey

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DURING NORMAL VISION our eyes make frequent, rapid movements (saccades) as we change fixation from point to point in the visual field. But our visual perception appears to be continuous and stable with no interruption or movement of the field associated with the rapid displacements of the image on the retina. Psychologists at the beginning of this century attributed this continuity in perception to a momentary blanking out of vision accompanying each rapid eye movement. Dodge (5) and Woodworth (20) viewed this perceptual blanking as an essentially passive effect resulting from the blurring of the retinal image during rapid movement and from one’s tendency to ignore such a blurred image. Holt (10) postulated that an active central inhibitory mechanism produced the perceptual blanking.

Several recent psychophysical experiments have shown that blanking is not absolute and that stimuli can be detected during a rapid eye movement under certain conditions. The threshold for detection of a dot pattern during a rapid eye movement was found to rise only 0.5 log units over the detection threshold for the stationary eye (17). Stimuli as complex as letters of the alphabet were recognized during a saccade if the brightness of the letters was well above threshold (16).

The question considered in this paper is what information is transmitted by the neurons of the visual system during rapid eye movements. Previous experiments have shown that, in the retinocortical branch of the visual system, information must reach at least as far as the visual cortex since many neurons in the striate cortex of the monkey continue to respond during rapid eye movements (21). The present experiments extend the study of the types of neuronal responses associated with rapid eye movements and investigate several characteristics of the stimulus sufficient to produce the responses. During these experiments the monkey first held its eyes stationary while the response of a striate cortex neuron to a stationary (or slowly moving) stimulus was determined; then the response of the neuron was determined while the monkey made a rapid eye movement across the same stimulus.

METHODS

Three rhesus monkeys, Macaca mulatta, were first trained to look at a small fixation light on a tangent screen 58 cm in front of them. Each time the monkey pressed a bar the fixation light appeared on the screen, remained on for a period which varied from 1 to 3 sec, and then dimmed for 400 msec. If the monkey released the bar during the dimming period it was rewarded with fruit juice or water. Details of this training method have been described previously (22).

The monkeys were then trained to make a 20° saccadic eye movement when the fixation light turned off and a second fixation light turned on at a point 20° away from the first light. Horizontal eye movements were elicited across the central part of the tangent screen which was about 70° wide and 90° high. In a typical sequence, a fixation light on the left turned on following a depression of the bar and then turned off 0.6 sec later as a second light on the right came on, and the monkey made a 20° saccade from left to right; then the light on the left came on again 2.0 sec later and the monkey made a 20° saccade from right to left. Either the first or the second fixation light could dim and the monkey was rewarded if it released the bar during the dimming pe-
riod. When the second fixation light dimmed, no return saccade was obtained, but dimming of the second fixation light was set to occur in less than 25% of the trials. A monkey well trained in the fixation task followed the shifting of the fixation light with very little additional training. There was a tendency for monkeys after this training to make anticipatory eye movements away from the fixation point. To correct this, it was occasionally necessary to retrain the monkeys on the initial fixation task. The eyes during fixation will be referred to as stationary even though in the awake animal the eyes were presumably always making the small movements of physiological nystagmus.

During recording, the methods for restraining the monkey, for recording of single units extracellularly, and for determining eye movements with an electrooculogram were the same as those used previously (4-6, 22). Once a unit was isolated, its receptive-field characteristics were determined while the eye was stationary during successive fixations. The types of units studied and the limitations on their analysis were the same as those described in the previous experiments on receptive fields (22). The units were all in the striate area (as determined by examination of the histological sections at the end of the experiment) and were in the deeper layers of the cortex. The receptive fields were between 3 and 10° from the fixation point and were (when receptive fields were determined) circular, simple, or more complex in organization. The possibility that some of the units were afferent fibers to cortex cannot be excluded. The location and approximate shape of the receptive field were determined for each unit so that a vigorous response to a stationary or slowly moving stimulus was always obtained, but the exact size and orientation of the receptive-field center were determined for only about half of the units. A circular spot or a slit of light effectively stimulated the central areas of the receptive fields studied.

During a rapid eye movement the stimulus light appeared at a point about halfway between the receptive-field positions at the two fixation points (Fig. 1). The stimulus was a slit of light with the same orientation and of about the same width but usually somewhat longer than the most effective stationary slit of light. When the effective stationary stimulus was a spot of light, the stimulus during a rapid eye movement was a vertical slit of light with a width equal to the diameter of the spot. Whatever stimulus was used during rapid eye movements had already been tested and found effective when the eyes were stationary. The stimulus was placed so that the receptive field of the cell was certain to cross it during the rapid eye movement. The slit of light was well above visual threshold: the background light was 1 cd/m² and the stimulus was 1-2 log units above that.

The response of a unit to the stimulus during rapid eye movement occurred against a background of spontaneous unit activity. To see the brief and sometimes variable response more clearly, it was useful to display together the unit discharges following each of a series of 20° eye movements. An amplitude discriminator converted the unit discharges to pulses and the pulses intensified the beam of the oscilloscope so that each unit discharge appeared as a dot. The eye movement triggered the sweep of the oscilloscope so that the responses following successive eye movements were lined up as successive rows of dots (10). A simple, digital logic circuit controlled the triggering so that a sweep occurred only when the stimulus light was on (or off for control periods with no stimulus) and when an eye movement of a given amplitude and direction occurred (detected by filtering the electrooculogram and capacity-coupling this filtered signal to a Schmidt trigger). Eye movement detection was not perfect, however, and spurious triggering occurred occasionally due either to noise in the electrooculogram record or to saccades different from the standard 20° movement. When it was useful to see the unit discharges before as well as after the eye movement, a digital delay line (designed by R. A. Newell and L. G. Letter) was used to delay the unit responses for up to 200 msec. The eye movement still triggered the sweep of the oscilloscope but the unit discharges following the eye movement were delayed and appeared near the center of the oscilloscope.
In the illustrations, a simple eye movement is shown above each raster. When the delay line was used, a photograph of both the electrooculogram and associated unit responses (without any delay) was made: the eye movement trace was then aligned above the raster by matching the unit pattern associated with the eye movement with the dot pattern on the single corresponding line of the raster.

Some units in the present study were included in one or both of two previous reports (21, 22).

RESULTS

Types of unit responses during rapid eye movements

The responses of 188 striate cortex units were examined. When an effective stimulus was stationary or slowly moving on the receptive field, each of the units showed an increase in its rate of discharge, and this will be referred to as an excitatory response. With rapid eye movements, the units could be placed into one of three categories (as reported previously (21)) based on the type of response produced by an effective stimulus as the receptive field of the unit passed over it. The three types were (1) an excitatory response, (2) no response, and (3) a suppression response. Examples of these response types are illustrated in parts A, B, and C of Fig. 2.

FIG. 2. Three types of unit response during a rapid eye movement. A sample electrooculogram of the 20° horizontal eye movement is shown for each to indicate occurrence of the rapid eye movement. Each unit discharge is represented by a dot, as is the beginning and end of each line. Successive lines are associated with successive eye movements. When the stimulus was present (upper sections of the three records) one unit showed an excitatory response (A, upper record), one showed no response (B, upper record), and one showed a suppression of response (C, upper record). When stimulus was absent (lower sections of the three records), none of the units responded during eye movement. All three units gave an excitatory response when stimulus was stationary or slowly moving on the receptive field. In this and subsequent figures, a downward deflection of eye movement record indicates a left-to-right eye movement, an upward deflection, right-to-left eye movement; divisions on time scale are 50 msec; 400 msec for the entire line.
The third group of units (37 units, 20% of the total) had their rate of discharge suppressed following a rapid eye movement (Fig. 2C, upper record). These units, like those of the first two groups, had given excitatory responses to a stationary or slowly moving stimulus. Three other units not included in these categories had inhibitory-center receptive fields, gave inhibitory responses to a stationary or slowly moving stimulus, and gave suppression responses following a rapid eye movement.

If no stimulus was present during a rapid eye movement, the units did not respond. For units of the first group, which gave excitatory responses following eye movements, the same 20° eye movements that were followed by a response when made across the stimulus (Fig. 2A, upper record) were followed by no response when made across a blank, evenly illuminated, white screen (Fig. 2A, lower record). The same lack of response following rapid eye movements across a blank screen was observed for units of the second group (Fig. 2B, lower record) and for those of the third group (Fig. 2C, lower record). Thus, in order to respond during rapid eye movements the striate cortex units required a patterned visual input just as they required such an input for maximum response when the eyes were stationary. Eye movement alone was not a sufficient condition to produce a response.

Although it was convenient to consider units in three groups, the classification was somewhat arbitrary. There was apparently a gradation between units showing either an excitatory or a suppression response and those showing no response. Samples of the responses of three units illustrate the gradation of excitatory responses following rapid eye movements (Fig. 3A). The response is clear for the unit shown on the left in Fig. 3A, clear but not so vigorous for the middle unit, and barely detectable for the unit on the right. A similar gradation of suppression is indicated by the three samples of unit responses in Fig. 3B. In addition, some units showed a second and opposite response following the initial response to the stimulus, and these units could have made up additional categories. The excitatory response was sometimes followed by a decrease in activity below the spontaneous rate, as suggested in Fig. 3A. The suppression response was sometimes followed by an increase in discharge rate, as in the unit response illustrated on the right in Fig. 3B.

**Stimulus information conveyed by excitatory-response units**

The slit of light used as the stimulus during a rapid eye movement was about the same width (usually about 0.5°) and somewhat longer than the most effective stationary stimulus for a unit. For 14 units that gave excitatory responses following

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**Fig. 3.** Examples of variation in response among units giving excitatory responses during rapid eye movements (A) and among units giving suppression responses during rapid eye movements (B). A clear response is on the left, a marginal response on the right in both A and B.
rapid eye movements, how specific the stimulus needed to be was estimated by changing one aspect of the stimulus—its width. Figure 4 shows the effect of increasing the width of a vertical slit of light from 0.5 to 5.5°. The response of this unit was better for narrower than for wider stimuli. For each of the units tested in this way some widths were more effective than others during rapid eye movements, just as some widths were more effective than others when the stimulus was stationary on the receptive field (although the best width was not necessarily the same during rest and movement). But with an eye movement, even with such a large change in stimulus width (by a factor of 10 in Fig. 4), the change in unit response was small compared with the change that occurred when the same alterations in stimulus width were made while the stimulus was stationary on the receptive field. Although the unit response following a rapid eye movement indicated the presence of the stimulus, the response did not indicate the width of the stimulus nearly so accurately as it did when the eyes were stationary.

When receptive fields were determined for units giving excitatory responses following rapid eye movements, some fields fell into each of the receptive-field categories determined in this experiment—circular, simple, and more complex. But the most vigorous responses with the most regular latencies following eye movements were from units having circular or simple receptive fields. The units responding best following rapid eye movements were those thought to be the lowest in the hierarchy of visual cortical neurons (12).

Units that responded to slow stimulus movement in one direction but showed no response or an inhibitory response to movement in the opposite direction also showed such selectivity if they responded when a rapid eye movement was made across the stimulus. For example, rapid eye movements to the right (across a vertical slit) were followed by excitation of a unit (Fig. 5A, top half) but eye movements to the left were followed by no response or a slight inhibition of unit activity (Fig. 5A, bottom half). But only five directionally selective units were found among those giving excitatory responses during rapid eye movements. Thus directional selectivity was shown by only 8% of the units giving an excitatory response during a rapid eye movement but by about 29% of the units giving an excitatory response when the eye was stationary. Although the sample of these units is very small, the result suggests that the type of unit showing directional selectivity for stimulus movement is poorly represented in the subsample of units which continue to give excitatory responses during rapid eye movement.

The great majority of units that gave excitatory responses during rapid eye movements responded to rapid horizontal eye movements in both directions across the stimulus. These units also responded to slow, horizontal stimulus movements in both directions across the receptive field. An example of the response of these neurons following rapid, horizontal eye movements is shown in Fig. 5B. Eye movements to the right across the stimulus (Fig. 5B, upper record) were followed by responses very
similar to those following eye movements to the left (Fig. 5B, lower record). There were always some differences in response to eye movement in the two directions (as in Fig. 5B), but such differences were difficult to estimate from the response of the unit to a slowly moving stimulus. For a few units of this same type it was possible to obtain both horizontal and vertical eye movements across the effective stimulus. The response following rapid eye movements was about what one would expect if one knew the response of the unit to a stimulus moving slowly on the receptive field. For example, a unit that gave an excitatory response following slow horizontal movements of a vertical slit also gave an excitatory response following rapid horizontal eye movements. For the same unit, movements of a horizontal slit up and down over the same receptive field produced little or no response, and vertical eye movements across a horizontal (or vertical) slit were followed by little response. Thus units that continued to give an excitatory response when the eye was moving continued to show the same specificity for movement that they had shown for a slowly moving stimulus when the eye was stationary.

Effect of textured stimuli on suppression response

One of the characteristics noted for the units giving a suppression of spontaneous discharge during a rapid eye movement was their apparent sensitivity to slight unevenness in illumination of the screen (21). The discharge rate was suppressed following eye movements over the stimulus (Fig. 6A). But the suppression response remained when the same eye movements were made with no stimulus present (Fig. 6B) and even when spontaneous eye movements of 20° or more were made (Fig. 6C). The screen in front of the monkey was not homogeneous but had dark areas of several degrees around the fixation light, and suppression could have resulted from these contrasts. This explanation seemed likely since spontaneous eye movements in total darkness produced no suppression (Fig. 6D).

That a nonhomogeneous area produced the suppression was confirmed when unit responses were recorded while eye movements were made across a white, evenly illuminated, homogeneous background. No suppression was observed (as illustrated in Fig. 5C, lower record), and it was concluded that the suppression of unit activity following rapid eye movements required the presence of some contrast in the visual field.

With the use of a homogeneous screen, it was possible to see whether a full-field, patterned stimulus was sufficient to produce the suppression response during an eye movement. The suppression response was clear during an eye movement when the specific stimulus was present (Fig. 7A), but when the same 20° eye movement was made...
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FIG. 6. Suppression response resulting from eye movements over a nonhomogeneous screen. Rapid eye movements across the stimulus were followed by a suppression of unit activity (A), as were the same eye movements across the nonhomogeneous screen without the stimulus (B). Spontaneous eye movements of 20° or of greater amplitude over the same screen also were followed by suppression response (C), but spontaneous eye movements made in the dark were not followed by any suppression (D).

FIG. 7. Suppression response resulting from eye movements over a textured stimulus covering the screen. A suppression response followed rapid eye movements across a slit of light 0.5 by 0.0° (A), but no suppression response followed eye movements across a white, homogenous screen (B). As shown in C and D, suppression responses followed eye movement across a textured stimulus covering the entire 70 x 30° screen in front of the monkeys.

across the white screen (Fig. 7B) there was no response. When texture was introduced, the suppression reappeared (Fig. 7C). The texture consisted of light dashes about 0.2° wide and up to several degrees long against a dark background, and the brightest areas were set to equal approximately the brightness of the clear white background, 1 cd/m². The textured stimulus covered the screen in front of the monkey (an area 70° wide and 90° high), and the horizontal eye movements were made across the central 20° of this area. The same textured stimulus viewed with a stationary eye produced no suppression. Suppression was also clear when rapid eye movements were made over a background of predominantly rounded light and dark areas (Fig. 7D). For the units giving an excitatory response during a rapid eye movement, an excitatory response to such a textured stimulus during a rapid eye movement was occasionally seen, but it was never so striking as the effect of the textured stimulus on the suppression units. For suppression units, a diffuse, textured stimulus appeared to be sufficient to elicit the suppression response during rapid eye movements.

What kind of contrast or pattern is
necesary to elicit the suppression response and over how large an area such a stimulus must extend has not been determined.

**DISCUSSION**

There are three principal findings in these experiments on the responses of striate cortex neurons during rapid eye movements. First, many neurons continue to respond to a stimulus during a rapid eye movement just as they do to a stationary or slowly moving stimulus. Second, the neurons studied apparently do not convey as much information about the stimulus during rapid eye movement as they do when the eye is stationary. Third, some neurons reverse from an excitatory response to a stimulus that is stationary or slowly moving on the receptive field to a suppression response to a stimulus during a rapid eye movement; these neurons respond to a non-specific, textured stimulus during a rapid eye movement.

No evidence is presently available on the function of these striate cortex neurons during a rapid eye movement. To judge what their significance might be, this discussion relates the characteristics of the cortical neurons in the monkey during rapid eye movements to perception in man during the same rapid eye movements. Limitations of this approach are that species differences between man and monkey are involved, that the behavioral output of the entire brain is being related to the response of a small fragment of it, and that within that small fragment are included only neurons with comparatively simple receptive fields located in the area surrounding the fovea.

The first finding is that many striate cortex neurons continue to respond during a rapid eye movement. Is there also perception during a rapid eye movement? Woodworth (20) was one of the first to argue that a stimulus can be detected during a rapid eye movement. He pointed out that when a rapid eye movement is made over a bright light with a dark background, the light is seen as a streak or a blur, and this effect can easily be demonstrated by moving one’s eyes rapidly across a standing spot on an oscilloscope screen in a darkened room. Ural and Smith (16) displayed a letter on the vertical axis of an oscilloscope so that it appeared as a bright vertical line to the stationary eye when the eye swept past the line the letter could be recognized. Thus it seems clear that when the stimulus is stationary and well above threshold it can be detected during a rapid eye movement. The stimuli used in the present experiments on cortical neurons were both stationary and well above threshold, and many of the neurons continued to give vigorous responses during rapid eye movements. There is no blanking out of the neuronal response, just as there apparently is no blanking out of perception under similar conditions.

The second finding is that striate cortex neurons seem to transmit less information about the stimulus when the eye is moving rapidly than when the eye is stationary. Is perception also less precise during a rapid eye movement? Woodworth (20) reported that the image during a rapid eye movement was blurred or appeared as a streak. Subjects in the experiment of Ural and Smith (16) could recognize letters but with an overall accuracy as low as 40%, correct with a moderately bright display and 20%, correct with a dim display. For stimuli near threshold, Volkman (17) found a small decrease in acuity during a rapid eye movement but Krauskopf et al. did not (15). Differences have also been reported between the threshold for detection of a dimly lighted stimulus when the eye was moving and when the eye was stationary. Volkman (17) found a rise in threshold for detection of a dot pattern or for recognition of letters of 0.5 log unit over the detection threshold for the stationary eye. Other studies have found increases in threshold for stationary stimuli ranging up to 2.0 log units (1, 24), no detection of a moving stimulus (2, 9), or in one case no rise in threshold for detection of a light flash (18). There is no doubt that some decrease in perception of detail during a rapid eye movement occurs even for stimuli well above threshold, and this decrease seems to be accentuated for patterned stimuli that are near the threshold for detection.

The decreased stimulus information conveyed by the striate cortex neurons that continued to give an excitatory response...
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... during a rapid eye movement would seem to correspond to the decreased perception of detail. Large changes in stimulus width led to much smaller changes in the neuronal response when the eye was moving than when the eye was stationary; therefore the neurons must give less accurate information on the width of the stimulus during a rapid eye movement. If it is reasonable to assume that the response of the neuron to stimulus width is related to acuity (11), the reduced neuronal sensitivity to stimulus width during a rapid eye movement is consistent with the decrease in acuity. In addition, among neurons giving an excitatory response during a rapid eye movement, those with the simplest types of receptive fields responded best during a rapid eye movement. The decreased response during rapid eye movements of the neurons thought to be higher in the sequence of visual cortical neurons (those with complex and hypercomplex receptive fields (12)) would seem to indicate a reduction of further processing of visual information at these higher levels; this is consistent with the increased ability of the individual to make discriminations. Finally, of the total sample of 188 neurons giving an excitatory response to a stimulus when the eye was stationary, about half did not respond at all to the stimulus during a rapid eye movement. The information conveyed by these neurons when the eye was stationary was lost completely when the eye was moving rapidly. Only about 30% continued to give an excitatory response during a rapid eye movement, and even these neurons responded less vigorously to a stimulus when the eye was moving than when the eye was stationary. Fewer neurons responding would seem to be consistent with the increased difficulty in perceiving the details of a bright stimulus and with the increased threshold for detecting a dim stimulus. The precision of stimulus movement perception is greatly reduced during a rapid eye movement (2, 9, 19). For example, a vertical displacement of a grid pattern by 0.5° was not detected at all during a horizontal rapid eye movement (9). In the present experiments only stationary stimuli were used but several characteristics of the neuronal responses observed during rapid eye movement may be relevant. There was a tendency for the neurons that showed the most specific response to stimulus movement (a response to movement in one direction but none to movement in the opposite direction) to respond poorly during rapid eye movement, and this might contribute to a less precise estimate of direction of motion. What would probably be even more important for detection of stimulus motion is the length of time that the stimulus is on the receptive field. One reason many neurons do not respond as the receptive field sweeps over the stimulus during a rapid eye movement might be that the stimulus is on the receptive field for too brief a time (23). If a stimulus movement perpendicular to the eye movement were added to the eye movement, then the stimulus would be on the receptive field for an even shorter time, and fewer units would be expected to respond.

The third finding of the present experiments is that some neurons are suppressed following rapid eye movement across a stimulus. How does this type of neuronal response fit with what is known about perception? The importance for perception of cues about movement that are contained in the visual image itself has been emphasized by Gibson (8). Relevant here is his suggestion that movement of the eye is indicated in part by a translation of the whole textured background with respect to the retina (7). In contrast to eye movement, object movement in front of the stationary eye is indicated by a localized moving area against a stationary, textured background (7).

Two characteristics of the neurons showing a suppression response make them well suited to signal a rapid translation of the background with respect to the retina and, thereby, to provide some indication that a rapid eye movement has occurred. First, the neurons exhibit a dramatic change in response with rapid eye movement: with the eye stationary there is an excitatory response, with the eye moving rapidly there is a suppression response. Second, this suppression response does not require the presence of a specific stimulus but occurs with a nonspecific, textured, background stimulus. An indication of rapid displacement from one neuron would not be a unique indicator of eye movement since stimulus
movement also can produce the suppression effect (23). But suppression of activity in a number of neurons with receptive fields in different parts of the retina could indicate total background movement. These suppression units would provide no information when eye movements are made in the dark or against a homogeneous background in the light and would provide erroneous information when the entire background moves in front of the eye. And, in fact, under some of these conditions there are perceptual illusions of motion such as the autokinetic effect seen in total darkness (7, 8).

That the suppression response found in the striate cortex neurons of the monkey is not unique is indicated by recent experiments on nerve cells in the visual system of the cricket (15). The cells studied gave an excitatory response to movement of an object anywhere in the visual field of one eye. But their rate of discharge was suppressed when the cricket was moved passively across a complex visual environment. Little inhibition was produced when the cricket was moved past a homogeneous visual field.

The interesting similarity between the cricket and monkey neurons is that for the same neuron there is excitation under one stimulus condition (slow movement in the monkey, small-object movement in the cricket) whereas there is suppression under another condition (rapid eye movement across a textured background in the monkey, movement of the eye across a complex visual environment in the cricket). Both experiments indicate that information on movement of the eye is contained in the neuronal response to the visual stimulus itself.

So far in this discussion only such passive consequences of eye motion across a stimulus as retinal blurring and rapid translation of the background have been considered. Another very different view of the effect of eye movement is that there is a more active process occurring, such as the central inhibitory mechanism proposed by Holt (10). As postulated in this and other "corollary discharge" hypotheses, information that an eye movement is occurring is transmitted to sensory and association areas of the brain. One indication that such an active process may be present was found in many of the experiments on stimulus detection during rapid eye movement considered above: a rise in the threshold began before the eye started to move (1, 14, 24). The neurons studied in striate cortex did not respond with eye movement alone: eye movements made in total darkness or across a white, homogeneous screen never produced any discharge associated with the movement. On the other hand, eye movement still might be affecting these striate cortex neurons. About half of the 188 neurons did not respond at all when a rapid eye movement was made across a stimulus, and these might either be actively inhibited by such a corollary discharge or simply not respond when the image moves rapidly on the retina. In addition, the suppression response of some neurons might result either from an interaction between the response of the neuron to the stimulus and the response to a corollary discharge or simply from the rapid stimulus movement with respect to the retina. To determine whether such a corollary discharge is indicated by the activity of these striate cortex neurons would require comparing the response during a rapid eye movement across a stationary stimulus with the response during a rapid stimulus movement in front of a stationary eye. That comparison is the subject of the following paper.

SUMMARY

The response of striate cortex neurons to a stationary or slowly moving stimulus on the receptive field was first determined while the awake monkey held its eyes stationary during a period of fixation. A 20° rapid eye movement was then elicited and the response of the neurons was determined as the receptive field moved across the stationary stimulus.

The neurons gave an excitatory response when an effective stimulus was stationary or slowly moving on the receptive field. During the rapid eye movements across the same stimulus three types of neuronal responses were observed: an increase in discharge rate (an excitatory response), no change in discharge rate (no response), and a decrease in discharge rate (a suppression response). These response types seemed to form a
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Neurons that gave an excitatory response
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by neurons having circular or simple
receptive-field organizations. When direc-
tional selectivity was found in a neuron
during the slow movement of a stimulus, it
was also found during the rapid eye move-
ment if the neuron continued to show an

excitatory response; but few neurons that
showed such a response to movement in
one direction and none to movement in
the opposite direction continued to respond
during an eye movement. The response of the
cortical neurons in the monkey ap-
peared to be consistent with the psycho-
physical observations on man showing that
a stimulus may be detected during a rapid
eye movement but with decreased resolution
of detail.

Neurons that gave a suppression response
during rapid eye movements also gave a
suppression response when eye movements
 were made across a textured background
stimulus. Both because these neurons re-
sponded to a textured background and be-
cause they reversed their response from
excitation to a stationary stimulus to sup-
presence during rapid eye movements, these
neurons might provide some indication of
the occurrence of rapid eye movements.

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