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USE OF AN EXTRARETINAL SIGNAL BY MONKEY SUPERIOR COLLICULUS NEU--ETC(U)

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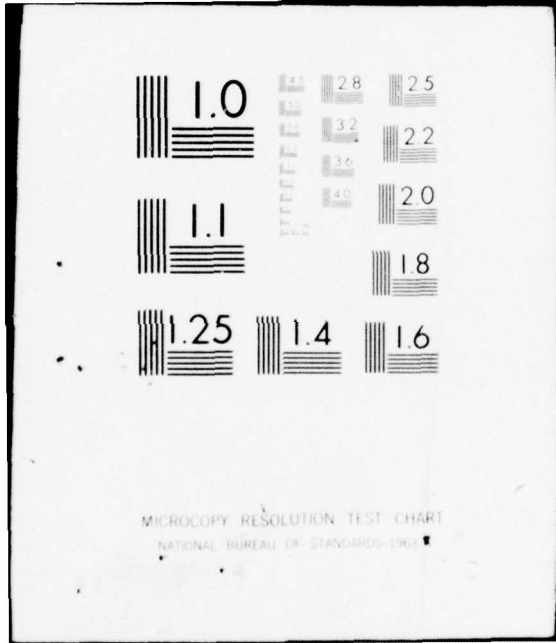
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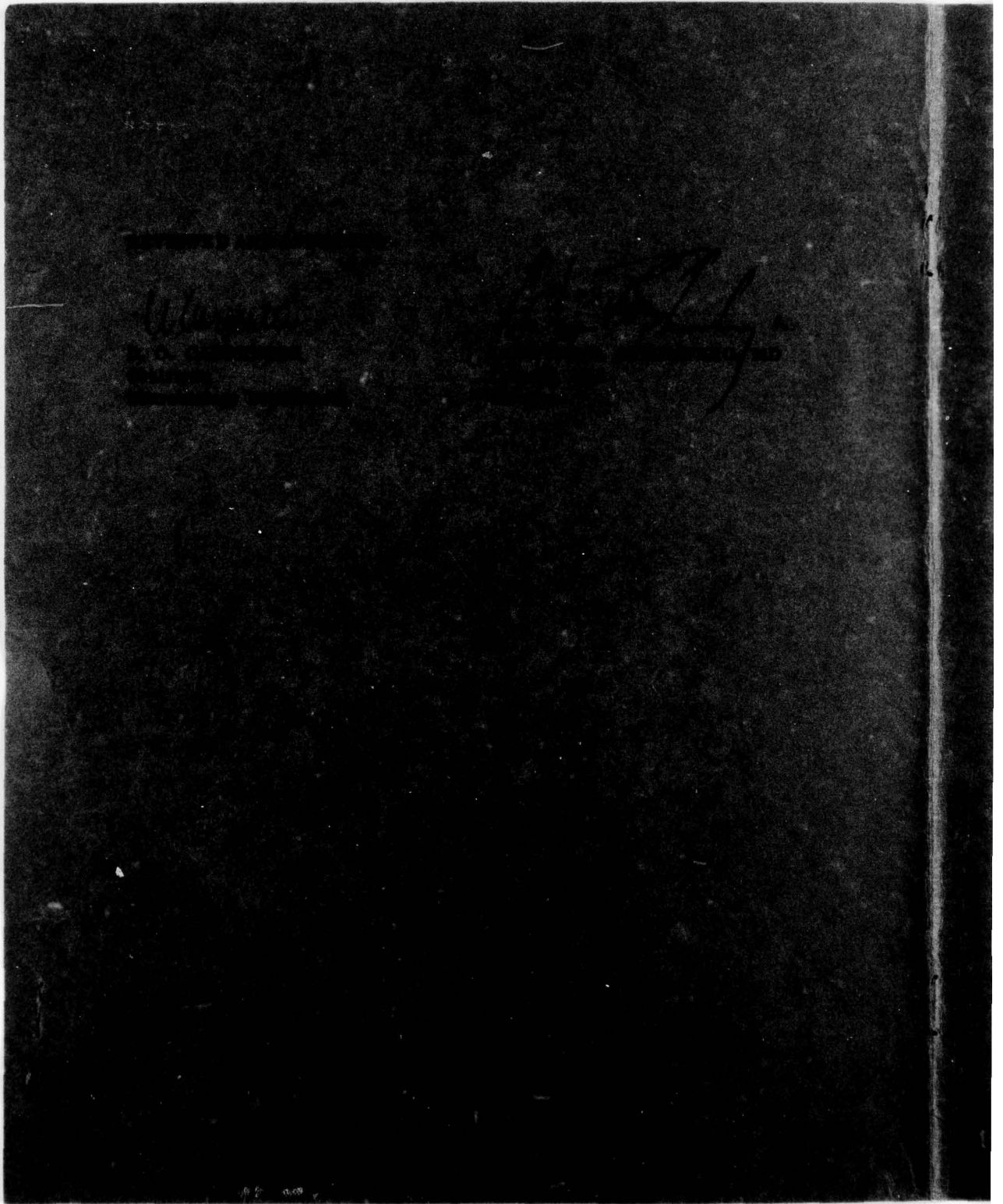


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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER AFRRI-SR76-28	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER ⑨
4. TITLE (and Subtitle) USE OF AN EXTRARETINAL SIGNAL BY MONKEY SUPERIOR COLLICULUS NEURONS TO DISTINGUISH REAL FROM SELF-INDUCED STIMULUS MOVEMENT.		5. TYPE OF REPORT & PERIOD COVERED Scientific rept.
7. AUTHOR(s) D. L./Robinson R. H./Wurtz (*National Institute of Mental Health)		8. CONTRACT OR GRANT NUMBER(s)
9. PERFORMING ORGANIZATION NAME AND ADDRESS Armed Forces Radiobiology Research Institute Defense Nuclear Agency (AFRRI) Bethesda, Maryland 20014		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS NWED QAXM C 912 23
11. CONTROLLING OFFICE NAME AND ADDRESS Director Defense Nuclear Agency (DNA) Washington, D. C. 20305		12. REPORT DATE June 1976
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office) 1248p.		13. NUMBER OF PAGES 50
16. DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited		15. SECURITY CLASS. (of this report) UNCLASSIFIED
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
18. SUPPLEMENTARY NOTES		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number)		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) We compared the response of superior colliculus cells to stimulus movement in front of the stationary eye with the response to stimulus movement generated by eye movement. Most cells responded to very high stimulus velocities in front of the stationary eye. The majority of these cells did not respond when an eye movement swept the receptive field over a stationary stimulus. This differentiation is present when the background illumination is reduced. For these cells, a suppression		

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20. ABSTRACT (continued)

of background activity is present following eye movements made in total darkness, indicating the presence of an extraretinal signal. The time course of this suppression matches the time at which visual effects would reach the colliculus. These cells also show a decreased responsiveness to visual stimulation during the background suppression. We conclude that these cells do not respond to stimulus movement during an eye movement because they receive this extraretinal signal. Such neurons also show an enhanced response to a visual stimulus when it is to be the target for a saccadic eye movement. This differentiation would provide an uncontaminated visual movement signal indicating real movement in the environment. Since the exploration of visual space is a basic component of visual perception, the understanding of the sensorimotor aspects of seeing can be applied to any situation where this is deranged, be that radiation damage, cerebrovascular disease, or head trauma.

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SUMMARY

In order to see whether cells in the superficial layers of the monkey superior colliculus can differentiate between real stimulus movement and self-induced stimulus movement we compared the discharge of these cells to stimulus movement in front of the stationary eye with stimulus movement generated by eye movements across a stationary stimulus.

Most of the cells recorded (65 percent of 231 cells) responded to stimulus velocities in front of the stationary eye as fast as those occurring during the peak velocity of a saccadic eye movement. Those cells that do respond usually have weak inhibitory regions and tend to have receptive fields farther from the fovea.

Most of the cells (61 percent of 105 cells) that did respond to rapid stimulus movement did not respond when an eye movement swept the receptive field over a stationary stimulus.

About half of these cells differentiated between these stimulus conditions when we used stimuli at least 1 log unit above background illumination; the remaining cells differentiated for stimuli 2 and 3 log units above background. Many cells differentiate between the two stimulus conditions over a wide range of directions of movement and the effect appears with about equal frequency in receptive fields at all distances from the fovea.

The differentiation is present for most cells even when the background illumination is reduced indicating that visual factors are not the cause of the effect on these cells but may modify the response of other cells.

The suppression of background activity accompanying eye movements in the light is present following eye movements made in total darkness; the suppression therefore must result from an extraretinal signal.

The failure of these cells to respond to visual stimulation during eye movements is due to the same extraretinal signal that produces the suppression since (1) the cells that show this suppression tend to be those that fail to respond to stimuli during eye movements, (2) the time course of the suppression

matches the time at which the effects of visual stimulation during an eye movement would reach the colliculus, and (3) the cells which differentiate also show a decreased responsiveness to visual stimulation during the time of background suppression. While this extraretinal signal has the characteristics one would expect of a corollary discharge, proprioception as a source of the signal cannot be excluded.

Cells which differentiate between the two stimulus conditions usually also show an enhanced response to a visual stimulus in their receptive field when it is to be the target for a saccadic eye movement.

→ These cells in the superior colliculus receive an extraretinal input which permits them to differentiate between real stimulus movements and stimulus movements resulting from the monkey's own eye movements. This differentiation would provide an uncontaminated visual movement signal and facilitate the detection of real movement in the environment. Such a process is consistent with the view that the colliculus is involved in selecting salient features of the environment and facilitating saccades to them.

PREFACE

These experiments were conducted while D. L. Robinson was supported by a postdoctoral fellowship from the Foundations' Fund for Research in Psychiatry.

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INTRODUCTION

How an animal distinguishes between the sensory stimulation produced by changes in his environment and other stimulation arising from his own movement has been debated for over a century. In the case of the eye, movement of a visual image on the retina can result from either the movement of an object in the world or of the eye itself across the visual scene.

Helmholtz³² suggested one mechanism for distinguishing real from self-induced movement: with each self-generated movement, the neural activity is directed not only to the muscles but also to the sensorium as a "sense of effort" to indicate that a movement has occurred and that subsequent sensory activity should be treated accordingly. von Holst⁵⁴ formalized this notion by suggesting that movement of an animal produced an "efference copy" which is used to discriminate self-induced stimulation, "reafference", from stimulation originating outside, "exafference". The term "corollary discharge" has also been used to describe this efference copy concept⁵² (see Teuber⁵³ for review). It should be noted that while the effects of these processes are usually thought of as modifying conscious perception, this need not be their only effect.²² For example, the term "efference copy" was originally used in discussing the optomotor behavior of insects,⁵⁴ while the term "corollary discharge" was first invoked when the forced circling of fish following eye rotation was considered.⁵²

This differentiation between exafference and reafference could also be derived from information about eye movements obtained from proprioceptors in the extraocular muscles. Thus while the differentiation would still be derived from an extraretinal signal (one arising from a source other than the visual stimulation of the retina), it would not require any efference copy or corollary discharge mechanism.

Finally, such a differentiation between real and self-induced stimulus movement need not involve any extraretinal signal at all. The differentiation could be derived from the fact that an eye movement produces a sweep of the

whole visual field across the retina while a stimulus movement usually involves only the movement of an object across the retina against a stationary visual field.^{27, 35}

In the primate visual system Wurtz⁵⁸ found that cells in striate cortex did not distinguish between visual stimulation due to eye movement and that due to external stimulus movement. Any differential effect seen in these two stimulus conditions would be accounted for by the movement of the visual background during an eye movement, so that neither corollary discharge nor proprioceptive feedback need be invoked to explain the observations. Recently, however, modulation of background activity of striate cortical neurons after eye movements has been demonstrated by averaging over many eye movements;^{19, 34} this effect may be too small to influence the response of cortical cells to the fairly weak stimulation used by Wurtz.⁵⁸

In contrast to these slight changes in activity in the striate cortex during eye movement, Goldberg and Wurtz²⁹ found that some cells in the superficial layers of the superior colliculus which respond to visual stimuli also show a striking suppression of activity in association with eye movements. Since this suppression persists even in total darkness, the effect must result from an extraretinal signal (which could be either a corollary discharge or proprioceptive feedback) occurring during an eye movement.

In the present experiments we investigated what effect this suppression has on the response of collicular cells to stimuli presented during eye movements. We found that many collicular cells differentiate between externally generated and self-induced stimulus movements and that this differentiation results from an extraretinal signal. We believe that this process of differentiation provides the nervous system with information about stimulus movement which is uncontaminated by self-induced stimulus movement. Brief reports of these experiments have appeared previously.^{47, 48}

METHODS

Using procedures described previously,⁵⁶ monkeys were trained to press a bar to turn on a small spot of light on a tangent screen. The monkeys learned to fixate the spot of light which remained on for from 1.0 to 3.0 sec and then dimmed for 0.5 sec. If the monkey released the bar during the dim period, he received a drop of water.

We recorded from five mature male rhesus monkeys (*Macaca mulatta*), 3 to 6 kg in body weight. Each day the animal entered a primate chair, worked for water until satiated, and then returned to its cage at the end of the experimental session. Comparable volumes of water were made available to the animal on those days when we did not record. Daily observation of the animal's general physical appearance, body weight, and performance patterns indicated that the animals remained in good health and were maintaining adequate body hydration.

Under sodium pentobarbital anesthesia, a head restraint device,²¹ micro-electrode cylinder,²⁰ and silver-silver chloride electrooculogram electrodes¹¹ were placed in position several days prior to initiation of recording sessions. Recording procedures were the same as those described previously.^{29,42} In brief, single cells were recorded from glass insulated platinum-iridium microelectrodes which were advanced to and withdrawn from the superior colliculus each day by a hydraulic microdrive. Direct current electrooculograms were recorded from the chronically implanted electrodes above and below one eye for vertical electrooculograms and on the outer canthus of each eye for horizontal electrooculograms. Control of the monkey's behavior and data analysis were accomplished on-line with a PDP-12 computer as described previously.⁴²

In our experiments we first determined the position and boundaries of the visual receptive field of a cell by using stationary and moving stimuli. Next, we determined the response of the cell as a stimulus moved across the stationary receptive field (the stimulus movement condition, Figure 1A). Finally,

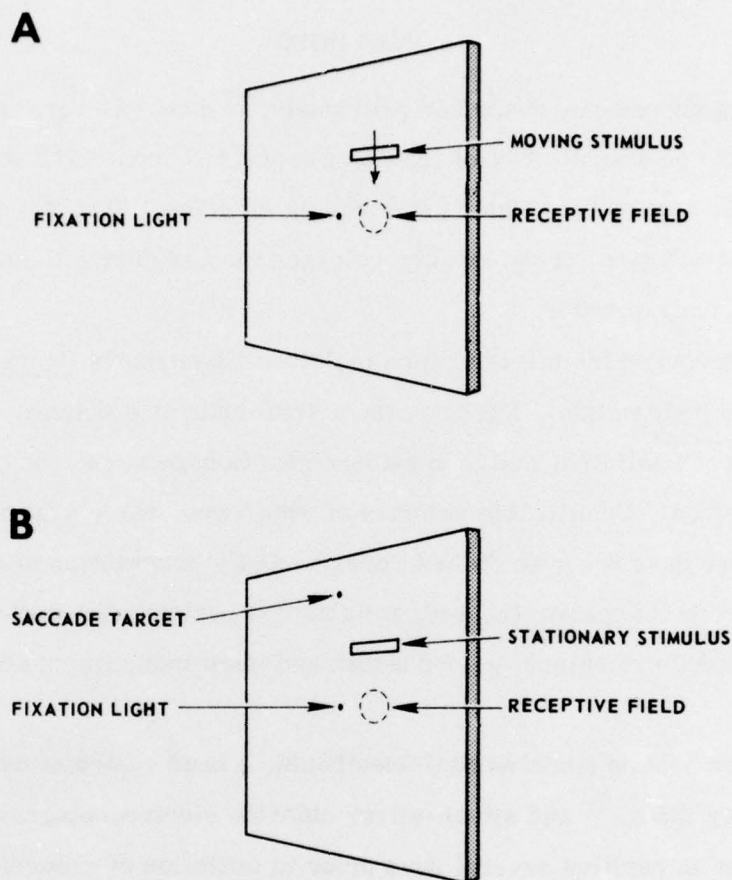


Figure 1. Schematic representation of the stimulus movement (A) and eye movement (B) experiments. A illustrates the tangent screen with the location of the fixation light, idealized visual receptive field, and position of the stimulus. The movement generator sweeps the stimulus over the stationary receptive field. B shows the same fixation light, receptive field, and stimulus position just prior to a saccadic eye movement to fixate the saccade target. The eye movement sweeps the receptive field over the stationary stimulus.

we determined the response of the cell as the eye moved the receptive field across the stationary stimulus (the eye movement condition, Figure 1B). Background illumination was 1 cd/m^2 and stimuli were 1 log unit above background.

In the first step, determining the response of the cell to rapid stimulus movement, we arranged to have the stimulus come onto the tangent screen 10°

from the edge of the visual receptive field as shown in Figure 1A. Each time the monkey fixated the spot of light, the stimulus came on at this position and then moved across the visual receptive field and off the tangent screen. Continuously variable stimulus velocities from 5 to 1000⁰/sec could be generated by this system. Velocities were calibrated by placing two photocells on the tangent screen 5⁰ apart and deriving the stimulus speed from the time interval between the two photocell signals. For some experiments we placed a single photocell on the screen at the edge of the visual receptive field so that a pulse from it would serve as a trigger.

In the second step, determining the response of a cell to self-induced stimulus movement, the stimulus remained stationary and the monkey moved the receptive field across it by making a saccadic eye movement from one point to another (Figure 1B). On these trials, the same fixation point came on after the monkey depressed the bar, and the same visual stimulus was projected onto the screen in the same location. Approximately 500 msec after the stimulus was flashed onto the screen, the fixation point went off and simultaneously a second spot of light, a saccade target, came on the screen 20⁰ from the fixation point. The disappearance of the fixation point and the appearance of the saccade target signaled the monkey to make a saccadic eye movement to this new target in order to fixate it. By making this eye movement, the monkey moved the visual receptive field of the cell over the stationary stimulus. Before doing the saccade experiment we checked to be sure that the stimulus was not in the receptive field or an inhibitory surround when the monkey fixated the fixation point or saccade target.

For comparison of stimulus movement in front of the stationary eye with eye movement across the stationary stimulus, we tried to keep the stimulus conditions comparable. The dimensions and position of the stimulus were the same in both cases. Its direction of movement, as seen by the retina, was the same since the stimulus was moved in one direction and the monkey made eye movements across the stimulus in the opposite direction. Since we placed the

stimulus approximately 10° from the edge of the visual receptive field and the monkey made a 20° eye movement, the visual receptive field crossed the stationary stimulus at the midpoint of the eye movement. The eye is at its maximum velocity at the midpoint of the saccade, and this velocity is approximately $900^{\circ}/\text{sec}$ for a 20° eye movement,²⁶ so we compared the response during the eye movement with that to a stimulus velocity of $900^{\circ}/\text{sec}$.

RESULTS

Response to rapid stimulus movement. We studied the response of 231 neurons in five monkeys to moving stimuli while the monkeys fixated. All of these cells had visual receptive fields and were comparable to those cells shown histologically to lie in the superficial layers (stratum zonale, stratum griseum superficiale, and stratum opticum) of the superior colliculus.²⁹ Almost all of these cells were of the type referred to as pandirectional;²⁹ they responded to small stationary spots of light projected anywhere within a large central excitatory region, frequently were inhibited by large visual stimuli covering and extending beyond this central region, and responded to stimulus motion in any direction across this excitatory area. Only a few cells showed any directional selectivity in their response to stimulus movement, and since the results of our experiments on these cells were identical to those of the pandirectional cells, we will not treat the directionally selective cells separately.

Our goal in these experiments was to compare the response of cells in the colliculus to a stimulus moving rapidly in front of the stationary eye (stimulus movement condition) to the response during a rapid eye movement across a stationary stimulus (eye movement condition). For a 20° saccade, the peak velocity is about $900^{\circ}/\text{sec}$;²⁶ longer saccades have peak velocities only slightly higher. We therefore first determined whether many collicular neurons responded to velocities as high as $900^{\circ}/\text{sec}$. We found that 65 percent of the collicular cells in our sample responded to a stimulus moving at such high velocities. The remaining 35 percent ceased responding at lower velocities or

responded to high velocities only erratically. The types of cell responses found are illustrated in the rasters in Figure 2. The cell discharges are represented by dots in the rasters, and the vertical line through the raster indicates the time when the stimulus crossed over a photocell placed adjacent to the central excitatory area of the receptive field. Successive horizontal lines indicate successive stimulations. Some cells responded to a spot of light swept across the receptive field of the cell at $20^{\circ}/\text{sec}$ (top raster, Figure 2A) and continued to give a clear response with stimulus velocities up to and including $900^{\circ}/\text{sec}$ (bottom raster, Figure 2A). Other cells, as shown in Figure 2B, also responded to stimulus velocities of $900^{\circ}/\text{sec}$ but only if an elongated stimulus was used. These cells presumably required a stimulus on the central excitatory area of the receptive field for a longer period of time to produce a response with high stimulus velocities. Finally, still other cells failed to respond, or responded erratically as in Figure 2C, to velocities of $900^{\circ}/\text{sec}$ no matter what type of stimulus configuration was used. No particular velocity cutoff was common across these cells, and we saw no indication of tight velocity tuning in any cells. Thus, there seems to be a continuum among these cells extending from those responding readily to rapid stimulus movement (Figure 2A) through those that respond begrudgingly if the stimulus size is optimal (Figure 2B) to those that do not respond no matter what the stimulus characteristics (Figure 2C).

On several occasions we observed that the response to stimulus movement consisted of a reduction of background firing prior to a burst of discharges (Figures 2A and C, 4A, 6A, and 12A). Since we tested to be certain that the stationary stimulus was not in an inhibitory surround of the cell prior to stimulus movement, the suppression is likely to result from an inhibitory part of the receptive field particularly sensitive to stimulus movement.

We found two variables related to whether or not a cell responded to high velocity stimulus movement. The first was the presence of a strong inhibitory region in the receptive field; cells which showed strong inhibition, as determined by the lack of response to large stationary stimuli, usually did not

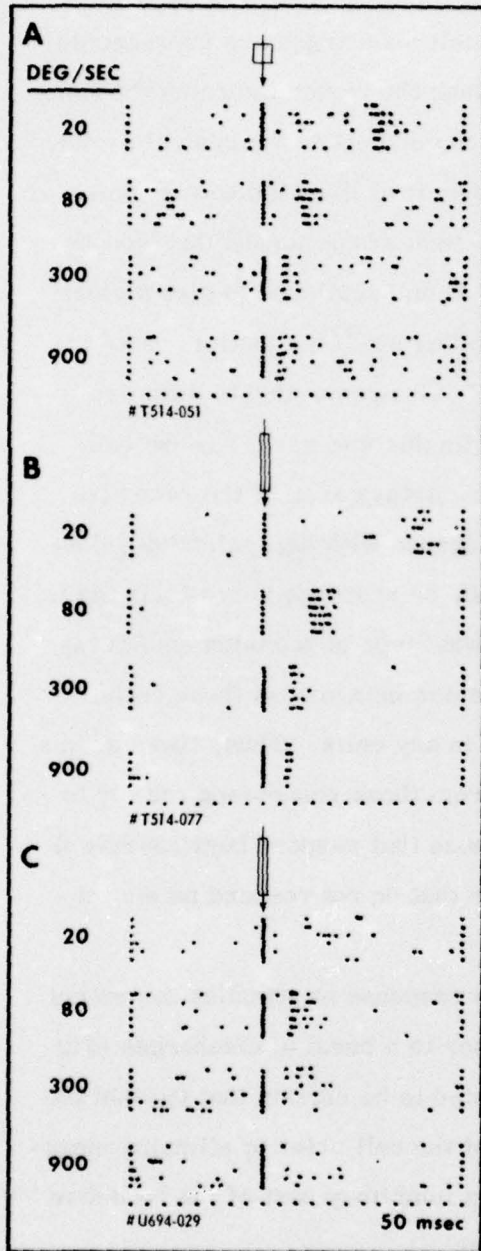


Figure 2.

Responses of three cells to increasingly rapid stimulus movement. In each raster, the dots correspond to spikes of the neuron, or beginning or end of a line. Successive rows of dots correspond to successive fixations by the monkey and a single sweep of the stimulus over the receptive field. Vertical line in each raster indicates the time of stimulus movement as indicated by a photocell trigger at the edge of the visual receptive field. The long interval between the trigger line and discharge seen for slower stimulus velocities is related to the time required for the stimulus to travel from the photocell to the excitatory area of the receptive field. In A, the cell continued to respond to a spot of light moved at low and high velocities (same cell as Figure 4A). In B, the stimulus had to be enlarged to produce such responses (same cell as Figure 4B), and in C, no stimulus was capable of consistently driving the cell at high velocities. Stimulus in A was $1.5 \times 1.5^\circ$ and in B and C, $3.0 \times 0.5^\circ$.

respond with rapid stimulus movement (as found in 13 of 14 neurons). The second factor was the position of the receptive field in the visual field. As shown in Figure 3A for our 231 neurons, cells with receptive fields farther from the fixation point had a greater tendency to respond to high velocity stimulus movement. Since receptive fields in monkey superior colliculus tend to be larger the farther away from the fovea they are located,^{16,29} this relationship could result simply from the fact that the stimulus stays on these larger fields for a longer time.

We were unable to find any cells which responded specifically to jerks of a stimulus in the receptive field.^{16,49} Cells that responded to such jerks of the

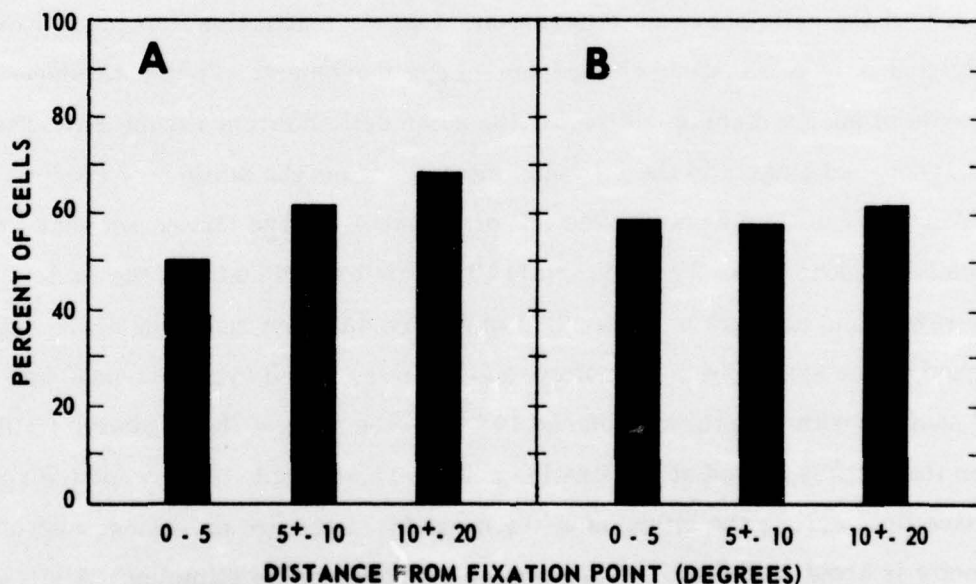


Figure 3. Responsiveness to rapid stimulus movement as a function of retinal eccentricity. A shows that the percentage of cells which respond to a stimulus moving at $900^{\circ}/\text{sec}$ increases slightly as a function of retinal eccentricity. B shows that the percentage of cells which differentiate externally generated from self-induced stimulus movement remains constant regardless of retinal eccentricity. Total of 231 cells for A and 105 cells for B.

stimulus responded as well to a stimulus swept across the field at a comparable velocity.

From these studies we can say that (1) many cells in the superior colliculus respond to rapid stimulus motion comparable to that occurring at the peak velocity of a saccadic eye movement, and (2) these cells that do respond usually have weak inhibitory regions and tend to have receptive fields farther from the fovea.

Differentiation between real and saccade-induced stimulus movements.

For those cells which we could drive with a stimulus swept rapidly over a stationary receptive field, we determined the response when a rapid eye movement (saccade) swept the receptive field over a stationary stimulus. Of the 105 neurons on which stimulus movement and eye movement conditions were tested, 61 percent of the cells showed a differentiation between stimulus movement externally generated and that resulting from an eye movement. Figure 4A shows an example of such a discrimination for the same cell shown in Figure 2A. The cell responded clearly to the stimulus moving across the stationary receptive field at $900^{\circ}/\text{sec}$, as shown on the left of Figure 4A. The histogram shows the summed responses for the same trials illustrated individually in the raster. The raster and histogram on the right of Figure 4A show the firing of the cell aligned on the start of a series of eye movements. Each eye movement was a 20° saccade with the stimulus placed 10° from the edge of the receptive field when the monkey looked at the fixation point. The saccade then swept the receptive field across the stimulus at the midpoint of the eye movement where the velocity is about $900^{\circ}/\text{sec}$. There was no response to the stimulus. A slight suppression of the discharge following eye movement is evident, and we will consider the characteristics and origin of this suppression later.

An example of the remaining 39 percent of the cells that did not show a clear differentiation is shown in Figure 4B. If any excitatory response was visible in the raster during an eye movement, we counted this as a lack of discrimination by the cell; our proportion of cells showing a differentiation therefore

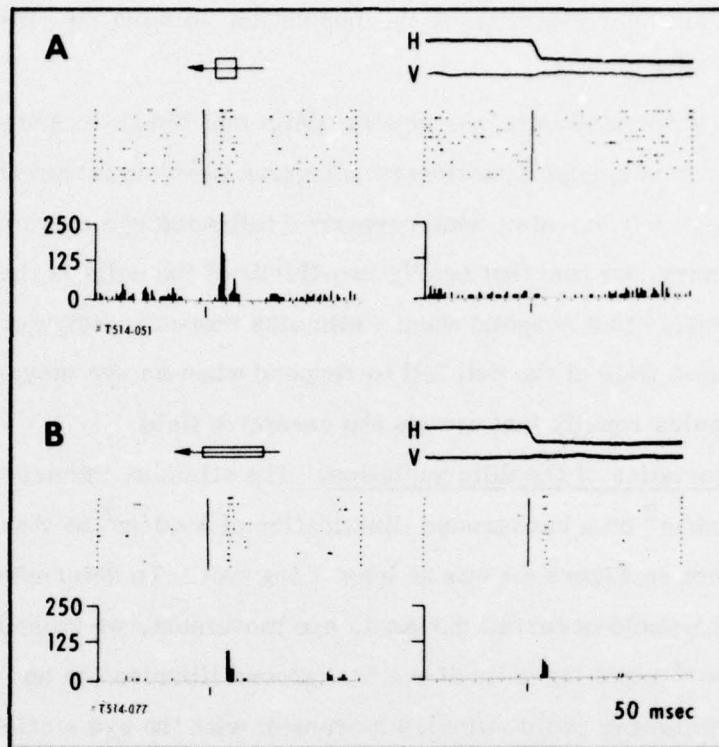


Figure 4. Response of a cell to stimulus movement in front of the stationary eye compared to the response to eye movement across a stationary stimulus. The cell in A differentiates between the two types of stimulus movement while the cell in B does not. A (left) shows the consistent response of a cell to a stimulus ($1.5 \times 1.5^\circ$) moving to the left across the receptive field at $900^\circ/\text{sec}$. Trigger for the raster and histogram is the time that the stimulus crossed the receptive field. A (right) shows the lack of response of the cell with a rightward saccade (as shown by representative horizontal (H) and vertical (V) electrooculograms). The trigger for the raster and histogram is the beginning of the eye movement as indicated by the initial deflection of the electrooculogram. Same cell as in Figure 2A. B shows similar data for a cell which responded to both types of stimulus movement. Stimulus was $3.0 \times 0.5^\circ$. Same cell as in Figure 2B. For this and all subsequent figures, an upward deflection on the horizontal electrooculogram corresponds to a leftward eye movement; and an upward deflection on the vertical electrooculogram indicates an upward eye movement. Histograms in this and all subsequent figures sum the trials in the adjacent raster. In all subsequent figures, stimulus movement is $900^\circ/\text{sec}$, time base is 50 msec between dots, vertical axis of histogram is 250 spikes/sec per trial, and bin width is 8 msec.

represents a minimal estimate of the population showing an effect of eye movement.

We also determined whether several cells that did not respond with rapid stimulus movement across a stationary receptive field might nonetheless respond during eye movements; none responded following eye movements.

In summary, we find that nearly two-thirds of the cells in the monkey superior colliculus that respond when a stimulus moves rapidly across the stationary receptive field of the cell fail to respond when an eye movement moves the same stimulus equally fast across the receptive field.

Characteristics of the differentiation. The stimulus intensity routinely used was 10 cd/m^2 on a background illumination of 1 cd/m^2 so that the suppression of response in Figure 4A was at least 1 log unit. To determine how much elevation of threshold occurred during an eye movement, we raised the stimulus intensity to 2 and 3 log units above background illumination and compared the response following rapid stimulus movement with the eye stationary and following rapid eye movement across the stationary stimulus. While some cells (9 of 21 so tested) which discriminated between the two stimulus conditions did so for stimuli as high as 2 or 3 log units above background (Figure 5A), most cells (12 of 21 tested) failed to differentiate when the stimulus intensity reached 2 log units above background (Figure 5B). Thus, the elevation of threshold is relative and varies among cells.

We next determined whether the differentiation between stimulus movement and eye movement conditions was selective for particular directions of eye movements. First, we found how a cell responded to rapid stimulus movement in four orthogonal directions. The great majority of the cells studied responded with stimulus movement in all directions although there might be a slightly better response with movements in some directions than in others (Figure 6A, for example). We then had the monkey make saccades so that his saccade moved the stimulus across the receptive field in the same direction as the previous experimenter-induced stimulus movement. We saw no response to the

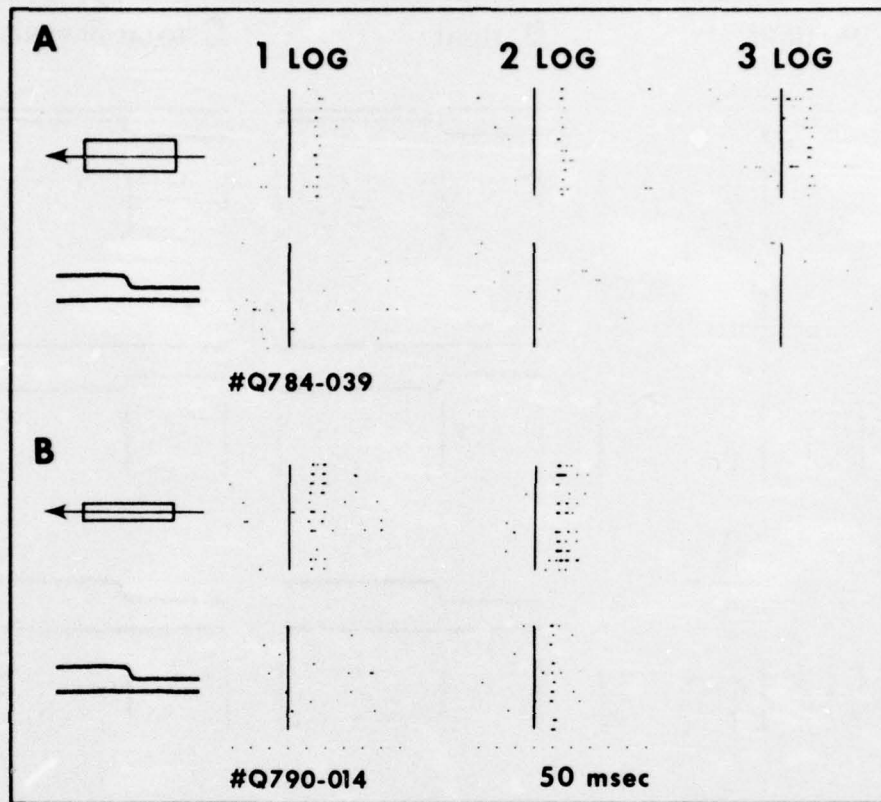


Figure 5. The effect of stimulus intensity on the ability of cells to differentiate between the two types of stimulus movement. Top row of rasters in A shows the response of a cell to rapid movement of a stimulus 1, 2, and 3 log units above the background illumination. Second row of rasters in A shows the lack of response of the cell to the stimulus at any of these intensities when the stimulus movement was generated by an eye movement. To change stimulus intensity from 2 to 3 log units, the background illumination was lowered 1 log unit. Stimulus was $3 \times 1^\circ$. The top row of rasters in B shows the response of another cell to rapid movement of a stimulus at 1 and 2 log units above background. Bottom rasters in B show that the stimulus movement resulting from eye movements elicited no response when the stimulus was 1 log unit above background but did when the stimulus was 2 log units above background. Stimulus was $3.0 \times 0.5^\circ$.

stimulus during an eye movement in any direction (Figure 6B). Of 16 cells tested in this manner, 8 did not respond with eye movements in any of the two to four directions tested. The remaining eight cells responded with eye movements in one or two directions (usually in the general direction of the receptive

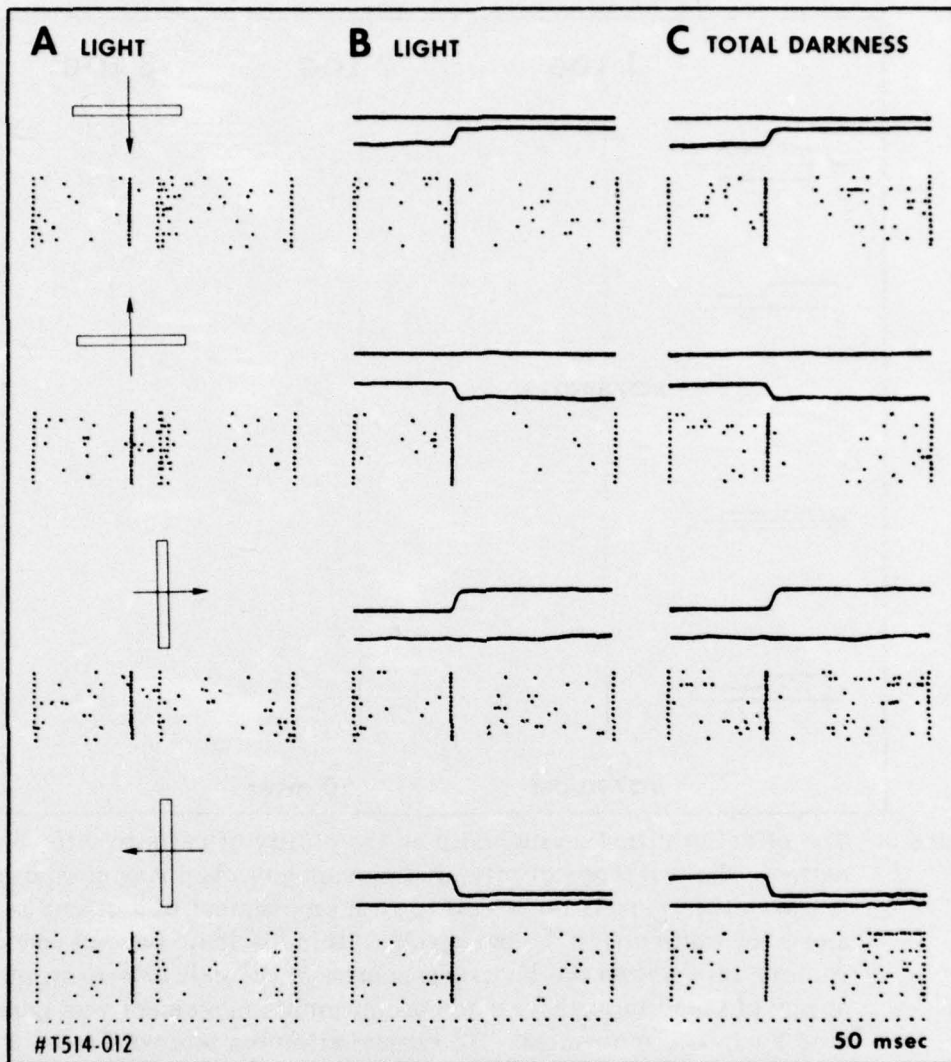


Figure 6. Lack of directionality in differentiation between the two types of stimulus movement. Column A shows the response of a cell to a stimulus ($7 \times 1^\circ$) moving in four directions. Column B shows the lack of response of the cell with eye movements in directions producing the same retinal motion as the stimulus movement to the left. Column C shows the suppression of discharge when similar eye movements were made spontaneously in total darkness.

field) but not with eye movements in the other directions tested. Therefore, the failure to respond to stimulus movement during an eye movement is not specific for saccades in one direction.

The cells which failed to respond to the stimulus during an eye movement had receptive fields in all parts of the visual field which were tested, that is, roughly 0.5° to 20.0° from the fixation point. While the proportion of cells responding to rapid stimulus movement in front of a stationary eye increased with the distance of the receptive field of the cell from the fovea (Figure 3A), the proportion of these neurons which distinguished between self-induced and external stimulus movement remained about the same for the 105 cells tested (Figure 3B).

Thus, we have determined three characteristics of the cells that distinguish between the stimulus movement condition and the eye movement condition: the failure to respond to the stimulus during an eye movement is typically an elevation of threshold of 1 log unit, but persists in some cells even when the stimulus is 2 or 3 log units above background, is clear following eye movements in several directions, and appears with about equal frequency in cells with receptive fields at all distances from the fovea.

Evidence for an extraretinal signal. While we have endeavored to produce stimulus movement across the receptive field of a cell that is identical in both the experimenter-induced and eye movement-induced cases, the experiments so far have not really succeeded in accomplishing that. In particular, when the eye moves, the entire visual field moves as well; when the stimulus moves, it does so against a stationary background. At this point we cannot exclude visually mediated suppression due to this background motion during a saccade as the mechanism which eliminates the response to a stimulus during an eye movement. To minimize the effect of such background movement, we ran the experiments with a stimulus intensity of 0.2 cd/m^2 against a darkened background. The only source of light was scatter from the fixation lights and receptive field stimuli themselves. Dark adaptation was minimized since the light indicating that the bar was disconnected came on for several seconds between successive fixation

periods. Figure 7 shows that the failure of a cell to respond to the stimulus during the eye movement in the light (Figure 7A) also occurred when the experiment was conducted in near darkness (Figure 7B). We did this experiment for 32 cells; for 25 of these cells (78 percent) we found results comparable to those shown in Figure 7. We conclude that for most collicular cells which discriminate, it is unlikely that the background movement associated with saccades is responsible for the failure of the cells to respond to the stimulus during the saccades.

There are two possible explanations for the response of the seven cells which discharged after an eye movement in the dark but not in the light. The

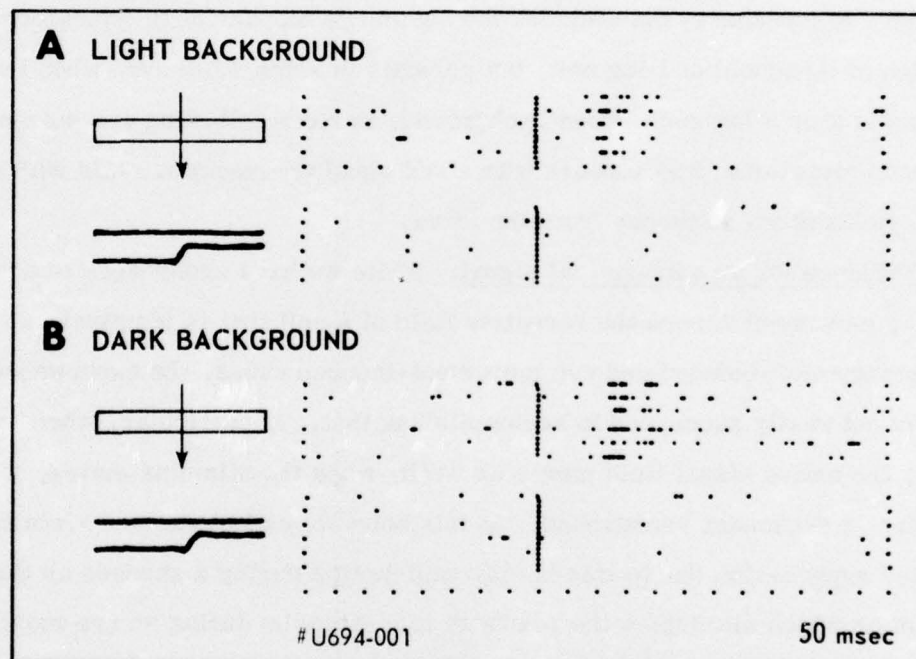


Figure 7. Persistence of differentiation between the two types of stimulus movement when visual factors were minimized. A shows the response of a cell to a stimulus (11×1^0) moving downward and the lack of response with an upward eye movement. Stimulus was 1 log unit above background illumination of 1 cd/m^2 . B shows the persistence of the differentiation between the two types of stimulus movement using a stimulus 0.2 cd/m^2 against an almost totally darkened background.

sharp contrast of the stimulus against the dark background might have produced a response stronger than any differentiation mechanism could eliminate. Alternatively, the movement of the background could have suppressed a response in the light, and the elimination of the visual background in the dark allowed the response. This would suggest that visual factors contribute to the activity of these collicular cells during an eye movement as they do in the geniculostriate system.^{39,57} We have no evidence to distinguish between these two alternatives for these cells but want to emphasize that visual factors may well contribute to the lack of discharge of a limited number of collicular cells during eye movements.

A suppression in the background rate of cell discharge associated with eye movements in the light (Figures 4A and 8A) was also present against a darkened background (Figures 7B and 12A). To determine whether such a suppression resulted from an extraretinal input, we placed the monkey in total darkness and looked for any suppression in cell discharge associated with spontaneous eye movements. We analyzed the activity of the cell in relation to spontaneous eye movements equal to those which were visually guided as well as those which deviated by $\pm 5-10^\circ$ from this standard. Selection was made automatically by the computer using a procedure described previously,⁴² and the light was turned on for 5 sec after every 15 sec in the dark in order to minimize the shift in the gain of the electrooculogram due to dark-adaptation (F. A. Miles and D. L. Robinson, unpublished observations). Figure 8 shows the results of such an experiment. For a cell which showed inhibition following eye movements in the light (Figure 8A), the inhibition persisted following saccades made in total darkness (Figure 8B; see also Figures 6, 9 and 12). This suppression is comparable to that reported previously by Goldberg and Wurtz.²⁹ Since the suppression is present in total darkness, we conclude that it indicates an extraretinal input to the visual cells in the superficial layers of the monkey superior colliculus.

Relationship of stimulus differentiation to suppression of background discharge. We next determined whether this extraretinal signal simply occurred at

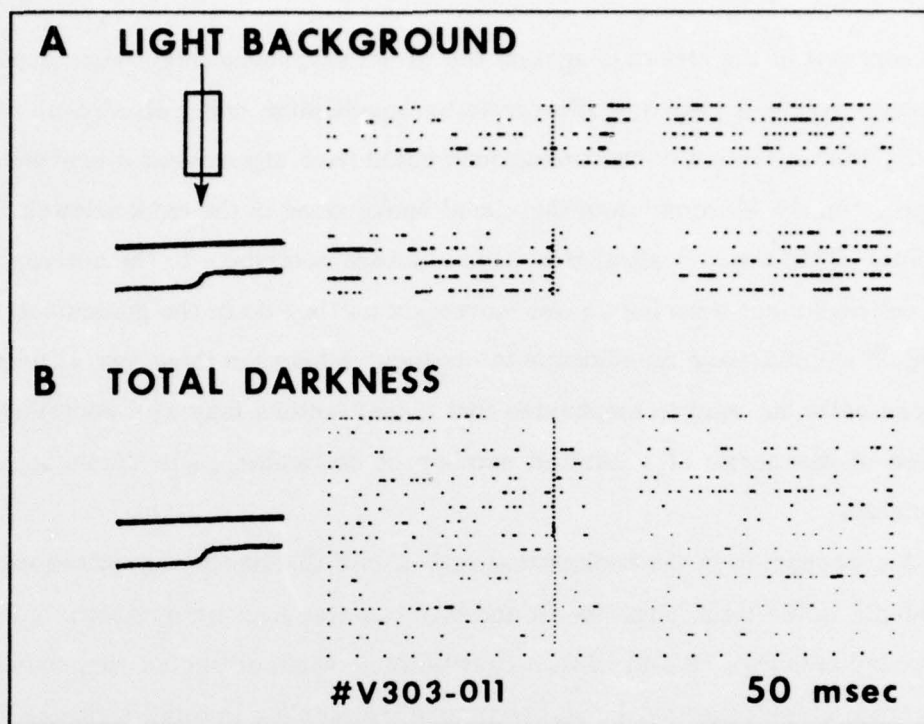


Figure 8. Evidence for an extraretinal input to a cell which differentiated between the two types of stimulus movement. A shows the response of the cell to a stimulus ($3.5 \times 1.5^\circ$) moving downward and the lack of response to the same stimulus with an upward eye movement. B shows the suppression of firing of the cell after upward saccadic eye movements made spontaneously in total darkness. The background discharge of the cell was decreased from about 60 msec to 175 msec after the start of the eye movement. Same cell as in Figure 12.

the same time as the lack of visual response with saccades or whether it might be responsible for this lack of response. We first checked to see if the suppression of background activity was more frequent in cells which did not respond to a stimulus during a saccade. We looked for this suppression following eye movements in 20 cells which had sufficiently high background rates to see a suppression on several raster lines and which failed to respond to the stimulus during an eye movement. We saw the suppression in all but one case. Enough samples of eye movements were obtained on three cells with low background rates of discharge to test for such suppression by averaging discharges for 30 to 60 eye

movements; in these cells we could also see indications of suppression following eye movements. In contrast to this, the discharge rate of 10 cells which responded to a stimulus during an eye movement and which had high rates of discharge showed no such suppression. We conclude that the suppression of firing following spontaneous eye movements in total darkness correlates well with the ability of the cell to distinguish between the stimulus movement and the eye movement conditions.

The suppression of the background rate of discharge was also similar to the lack of response to the stimulus during an eye movement in that it occurred with saccades in many directions (Figure 6C). We also found that the suppression was clear regardless of the amplitude of the saccade over the range of 10 to 30° (Figure 9). There was also a slight tendency for the suppression to be more prolonged with larger eye movements (compare Figure 9A-C).

More important to the comparison of the suppression to the lack of visual response is the relative time of occurrence of the two events. The duration of the suppression seen in the dark is shown graphically in Figure 10. The earliest onset of the suppression was at about the start of the electrooculogram deflection associated with an eye movement, but the average time was 40 msec after the start of the electrooculogram change. The longest duration was for 275 msec after the initial electrooculogram change with an average of 180 msec. This suppression would generally precede the response of collicular cells to visual stimuli since that occurs from 35 to 60 msec after light falls on the retina.⁶¹ Cells with a short latency response to visual stimulation and a long latency for the onset of suppression occasionally showed a slight visual response which was then cut off by the onset of the suppression, but in general, the suppression after an eye movement came at the same time as the response to the stimulus and could account for the reduced visual response during an eye movement.

If this suppression is responsible for eliminating the visual response to an eye movement, an effect should be evident on stimuli presented just after an eye movement; the suppression is always present 60 to 125 msec after the eye

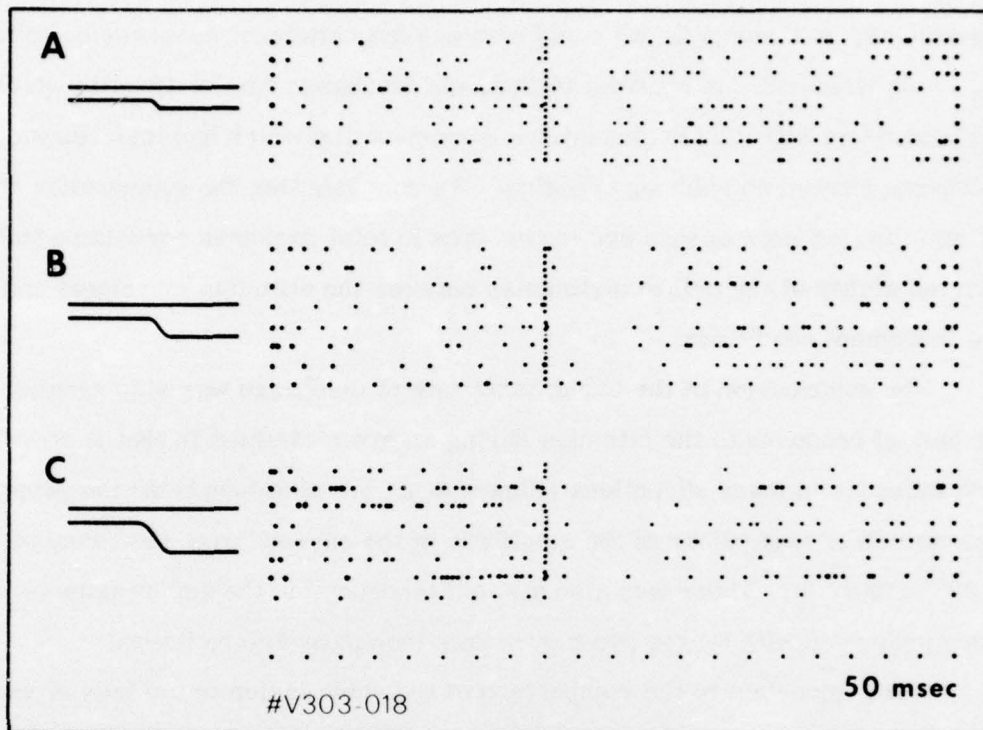


Figure 9. Relationship of the size of eye movements to the suppression of the background rate of the cell discharge. A illustrates the presence of the suppression of background discharge associated with $10^{\circ} (\pm 3^{\circ})$ eye movements in total darkness. B and C show the presence of the suppression with increasingly larger eye movements (20 and $30^{\circ} \pm 3^{\circ}$) and the tendency for the period of suppression to be prolonged with progressively larger eye movements.

movement as shown in Figure 10. In addition, such a test would eliminate any artifact related to eye movements across a stimulus since the stimulus is presented when the eye is actually stationary. To study this we conducted the following experiments against a darkened background on nine cells that differentiated between the two stimulus conditions. For these experiments we used the end of a saccade (from some point in the visual field to the fixation point) to trigger the sweep of the stimulus across the receptive field. This allowed us to test the responsiveness of the cells not during the eye movement but during the period of suppression after it. We found the sensitivity reduced. For example,

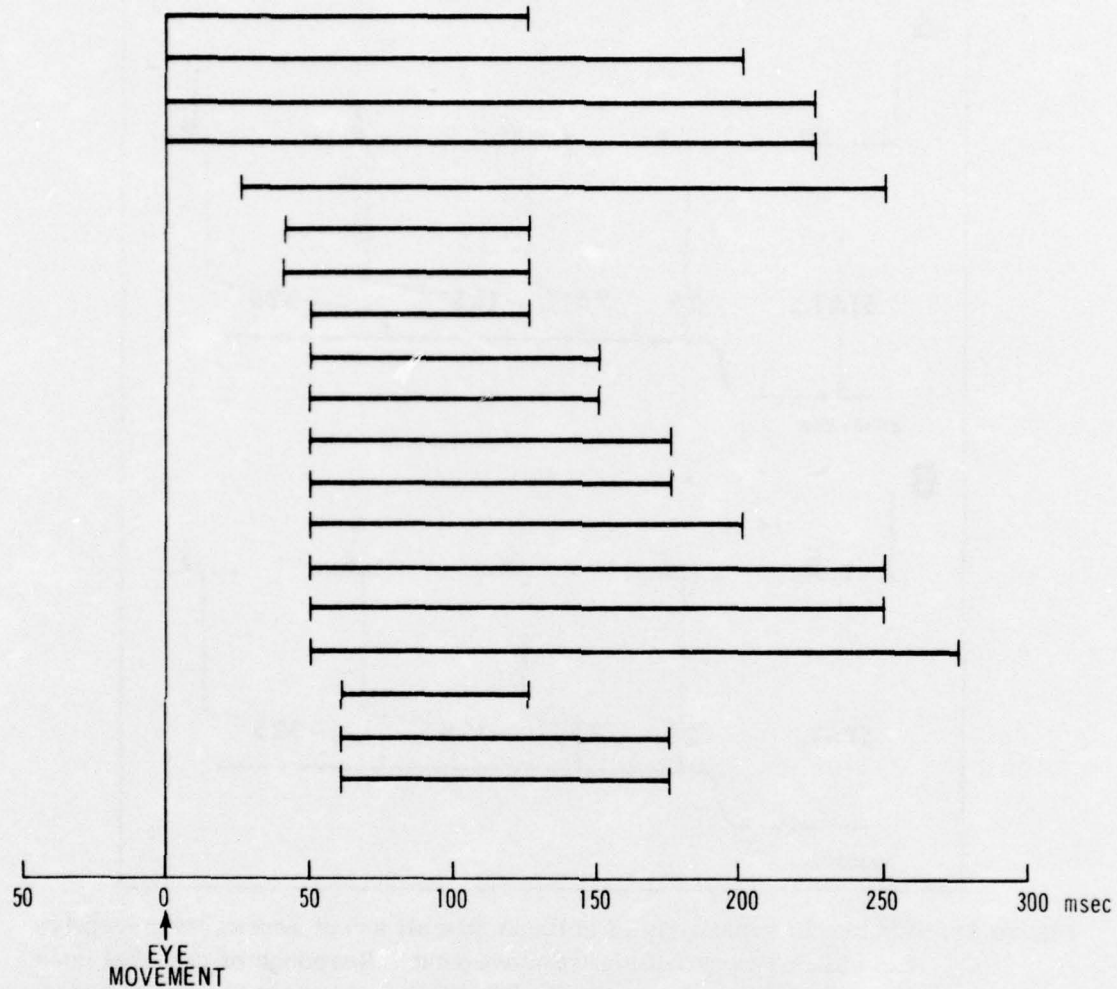


Figure 10. Timing of extraretinal suppression. Each horizontal line indicates the approximate beginning and duration of the suppression of background firing in association with spontaneous eye movements made in total darkness. Timing is synchronized relative to the beginning of the eye movement as indicated by the initial deflection of the electrooculogram.

in Figure 11A, the response to the visual stimulus is reduced when it is on the receptive field 25 and 75 msec after the eye movement, but it is back to normal by 125 msec. The suppressive effect of the eye movement clearly becomes weaker after the eye movement; the effect eliminates any response to the stimuli

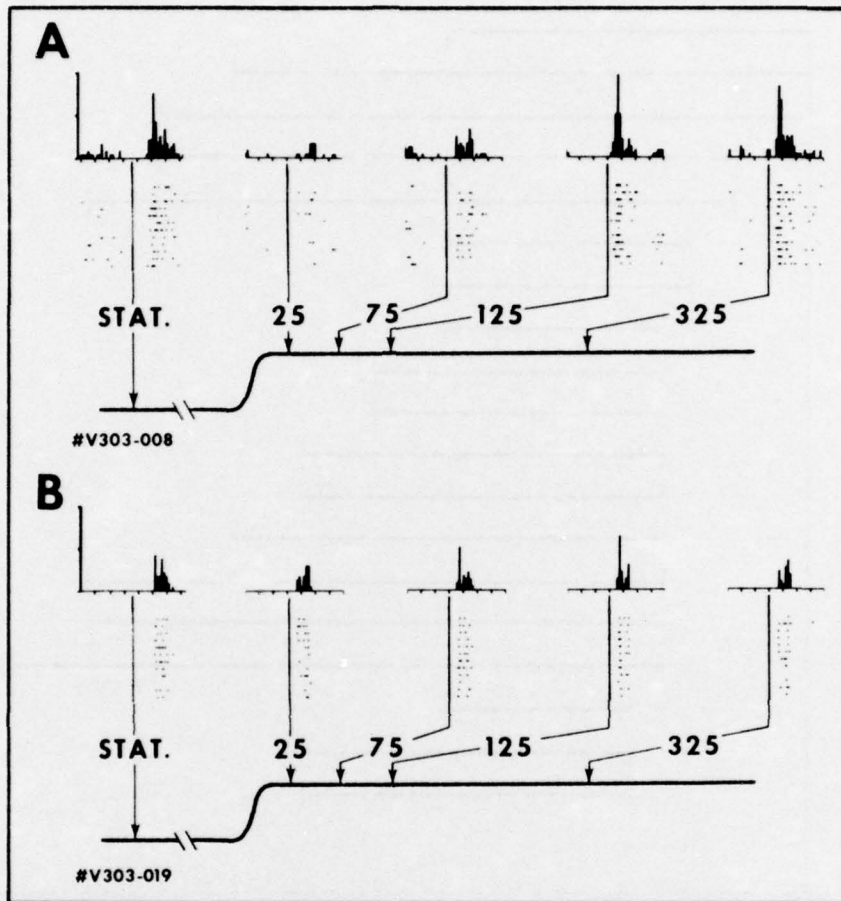


Figure 11. Change in sensitivity of cells to stimuli swept across the receptive field after the end of an eye movement. Response of cell that does (A) and cell that does not (B) differentiate between the two types of stimulus movement. Rasters and histograms on the far left (STAT.) show the response of the cells to rapid stimulus movement while the animal fixates. Subsequent histograms and rasters show the response of the cells to the same stimulus swept across the receptive field at progressively later times (25, 75, 125 and 325 msec) after the end of the eye movement. Histogram and raster time bases are 50 msec. Experiments were conducted in near total darkness with stimuli of 0.2 cd/m^2 . The cell in A shows a decreased excitability after the eye movement; the cell in B does not.

when they cross the visual receptive field during the eye movement, can reduce visual responses for short intervals after the eye movement, and gradually becomes ineffective at later times.

We conducted comparable experiments on seven cells which did not differentiate between the two types of stimulus movement, and six of them had no response reduction after eye movements. An example of such a cell is shown in Figure 11B. The remaining cell had a response reduction only at our test interval 25 msec after the eye movement. This interval was so brief that to see the differentiation in our standard experiment would require the conditions to be very exact. With the possible exception of this neuron, the cells which differentiate between the two types of stimulus movement also show a reduced sensitivity to visual stimuli after the eye movement; those that do not differentiate, do not show the reduced sensitivity.

Since our primary concern is with stimulus movement, we routinely studied posteye movement suppression using moving stimuli. However, we did test posteye movement suppression for some cells with both stationary and moving stimuli; five of seven cells had comparable results for both conditions. The remaining two neurons showed response reduction to moving but not to flashed stimuli. The lack of perfect agreement for the two conditions may reflect differences in the responsiveness of these cells to moving and stationary stimuli.

For seven neurons we compared the time course of the response reduction to stimulus movement after an eye movement with the time course of suppression after spontaneous eye movements in total darkness. The time courses of both effects were roughly parallel. Cells with brief rate suppression after spontaneous eye movements had brief intervals of response reduction to stimulus movement; the converse was true for long suppressions. For example, in Figure 12, the suppression of background rate lasts about 115 msec after spontaneous eye movements in total darkness (Figure 12C), but 70 msec after visually triggered eye movements (Figure 12A). As the stimulus crossed the receptive field close to this period, the response to it declined (Figure 12B). The prolonged suppression of firing after eye movements in total darkness compared with the reduced responsiveness to stimulus movement after eye movements was typical; it suggests that the strength of the inhibition tapers off near its end and

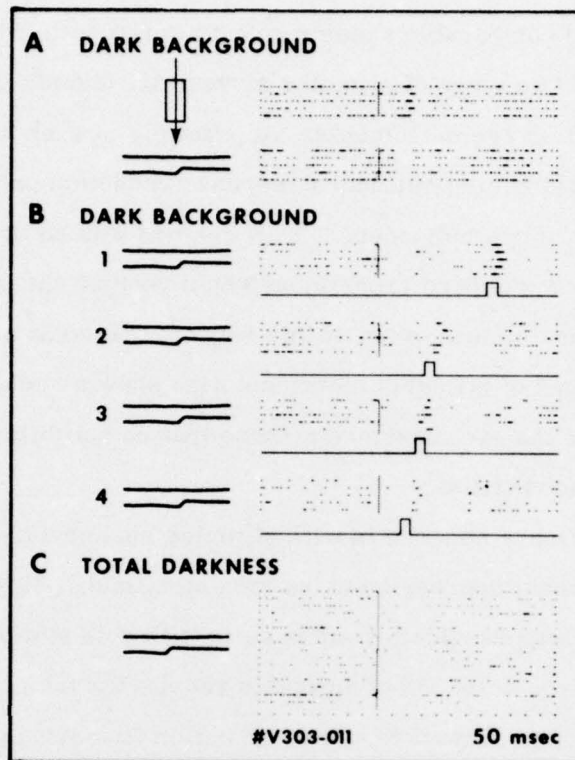


Figure 12. Synchrony of suppression of background activity and decrease in excitability to visual stimulation of a cell which differentiates between the two stimulus movement conditions. A illustrates the response of the cell to externally generated stimulus movement and lack of response when the stimulus movement is generated by an eye movement. The stimulus was $3.5 \times 1.5^\circ$ and intensity was 0.2 cd/m^2 with background of almost total darkness. B shows the narrow postsaccade time interval within which the effects of stimulus movement are reduced. Vertical lines within each of these rasters indicate the beginning of the 20° upward eye movement. Indicator line below each raster marks the time when the stimulus (same as in A) was swept across the receptive field after the eye movement. Same cell as in Figure 8. Delays were 325, 125, 75 and 25 msec after the end of the eye movement. C shows the time interval during which firing of the cell was suppressed in association with similar spontaneous eye movements made in total darkness. The period of suppression in C coincides with the interval of decreased responsiveness of the cell seen in B but does not appear to be as narrow as in A, presumably because of the reduction in background firing.

is not then sufficiently strong in that period to eliminate the excitatory response to a stimulus.

We conclude that the same extraretinal signal which produces the suppression of background activity after an eye movement reduces the response of the cell to stimuli during an eye movement since (1) cells that show suppression tend to be the same cells that fail to respond to stimuli during eye movement, (2) the time course of the suppression matches the time that visual stimulation during an eye movement would reach the colliculus, and (3) the cells which differentiate also show a decreased responsiveness to visual stimuli during the time of background suppression.

Relationship of stimulus differentiation to response enhancement. Goldberg and Wurtz³⁰ found that cells in the superficial layers of the superior colliculus have an enhanced response to a visual stimulus when that stimulus is to be the target for a saccadic eye movement. We have tested for this enhancement effect on six cells that differentiated between the two types of stimulus movement and on which we have other data confirming the existence of an extraretinal signal (suppression of rate of discharge with eye movements in total darkness or reduced responsiveness to stimulus movement after an eye movement). All six showed the enhancement effect. For example, the cell in Figure 13 shows both a differentiation between rapid stimulus movement in front of the stationary eye and rapid eye movement across the stationary stimulus (Figure 13A) and an enhanced response when the monkey uses the receptive field stimulus as the target for an eye movement (Figure 13B).

Cells which do not differentiate between the two stimulus conditions or those which do but have no other evidence of an extraretinal signal generally do not show the enhancement effect (16 of 17 cells). Thus, it appears that cells which differentiate between the two stimulus movement conditions frequently show the enhancement effect; whether these two effects are always present in the same cells cannot be determined from our small sample of neurons.

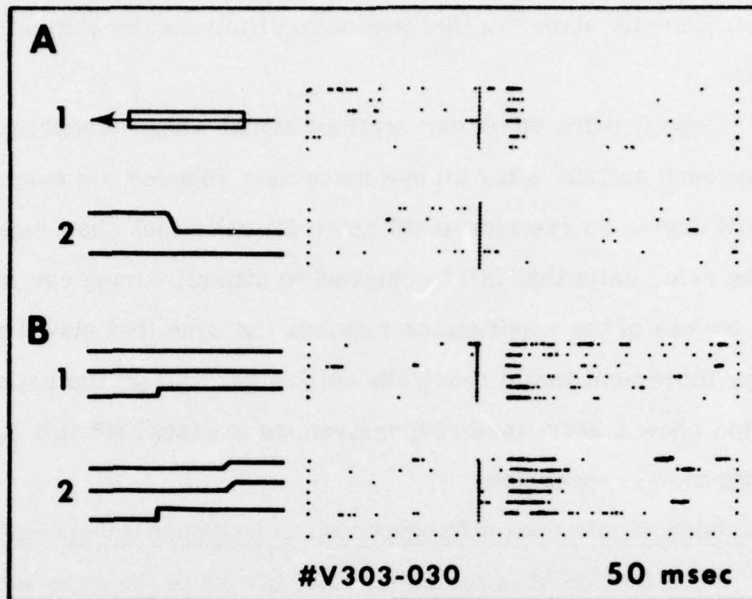


Figure 13. Response of a cell which differentiates between the two types of stimulus movement and shows response enhancement. A1 illustrates the response of the cell to rapid leftward movement of a stimulus ($4.0 \times 0.5^\circ$) and A2 shows the lack of response when stimulus movement is caused by a rightward eye movement. This cell also had a reduced responsiveness to stimulus movement after eye movements and a suppression of discharge rate after spontaneous eye movements in total darkness. B shows the enhanced response of the cell when the monkey used the visual receptive field stimulus as the target for a saccadic eye movement. B1 shows the response of the cell to a stationary stimulus ($0.5 \times 0.5^\circ$) in the visual receptive field (4° left, 3° up) while the animal fixates. Top two traces to the left of the raster show schematic horizontal and vertical electrooculograms prior to and after stimulus onset which is indicated by the step in the third trace. B2 shows the enhanced response to the same stimulus when it is to be the target for a saccadic eye movement. Step in the bottom trace of B2 indicates the onset of the stimulus in the visual receptive field to which the animal made an eye movement (4° left, 3° up) as indicated by the deflections on the electrooculogram traces.

Wurtz and Mohler⁶¹ found that for some cells a response enhancement can be demonstrated following as well as prior to an eye movement toward the receptive field. Thus, for cells which differentiate and have the enhancement

effect, we would expect that these suppressive and facilitory effects would be pitted against each other for eye movements directed into and around the receptive field. Such postsaccadic enhancement effects might account for the slight response to a stimulus with certain directions of eye movements, but at present we have no other data on the interaction of the two effects.

DISCUSSION

Our experiments have demonstrated for the first time that neurons in a primate sensory system can differentiate between real and self-induced stimulation. Furthermore, we think that this discrimination is caused by a modification of activity by a signal generated outside the receptor organ itself. In brief, we have found (1) that many cells in the superficial layers of the superior colliculus which respond to rapid stimulus movement in front of a stationary eye do not respond when a rapid eye movement sweeps the receptive field across a stationary stimulus; (2) that a suppression of background activity which accompanies these eye movements results from an extraretinal signal; and (3) that the lack of response of these cells to stimuli during an eye movement results from this extraretinal input. We will discuss these findings in relation to the nature of the extraretinal input, the origin of the input, a comparison with striate cortex, and the functional implications of the effect.

Differentiation as a result of an extraretinal signal. Most of the cells that respond to externally generated stimulus movement do not respond when the image movement across the retina is generated by an eye movement. It is possible that this lack of response with eye movements is caused by visual factors, e. g., movement of the visual background during an eye movement as has been demonstrated in psychophysical^{35,38} and electrophysiological experiments.^{2,24,25,39,57} Several experiments suggest that this is not the case for these superior colliculus neurons. When cells are studied with the monkey in a darkened environment, thereby reducing the influence of visual factors, the differentiation persists (Figure 7). In addition, many neurons which differentiate

have enough spontaneous firing to test for changes in activity in association with eye movements in total darkness, thereby eliminating visual factors entirely. These cells show a suppression of firing after eye movements in the dark (Figures 6, 8, 9 and 12). Since this suppression occurs in total darkness it must result from an extraretinal signal.

We believe that the extraretinal signal responsible for this suppression is likely also to be responsible for the lack of visual response during an eye movement. First, the cells that show the suppression tend to be those that do not respond to the stimulus during saccades; those that show no suppression do respond to the stimulus during saccades. Second, the time course of the suppression is such that it is consistently present when the visual responses resulting from retinal stimulation during an eye movement would reach the colliculus (Figure 10). Third, the visual excitability of these cells which differentiate (as determined by the response of the cell to a moving stimulus) was decreased during the time after the saccade when the suppression was clearest (Figure 11A). Again, the cells we tested which did not show the differentiation between the two stimulus conditions did not show this decreased visual responsiveness after the eye movement (Figure 11B). Thus while each experiment by itself is probably not conclusive, we think that the set of observations described provides strong support for an extraretinal signal as the source of this differentiation between stimulus movement and eye movement conditions as well as the suppression of background activity. We conclude that these cells in the monkey superior colliculus receive both visual and eye movement related inputs; the eye movement related input can suppress the visual input when they occur simultaneously.

Sources of the extraretinal signal. There are a number of potential sources of this extraretinal signal. The first one to consider is the mechanical stimulation of the retina due to the lag of the vitreous fluid as the eye turns rapidly.⁴⁴ This stimulation, which is extraretinal only in the extravisual sense in which we have used the term, seems unlikely to produce the suppression in the colliculus. First, the suppression effect occurs with a short latency in many

cells while the conduction time through the retina to the colliculus takes at least 35 msec. Any effect from a mechanical shearing of the retina would have to act on the ganglion cells to produce the short latency suppression. Second, we see a clear suppression in the colliculus but nothing so dramatic in striate cortex;⁵⁷ if the effect were due to a mechanical stimulation of the retina, fibers to both structures should be affected, particularly since retinal ganglion cell axons branch to both structures.¹³

Since we have never seen a compelling example of suppression which precedes the deflection of the electrooculogram, there is also the possibility that activity from proprioceptive end organs of the extraocular muscles could cause this suppression. Several electrophysiological experiments have demonstrated the existence of connections from muscle stretch receptors to the colliculus.^{1, 14, 15, 23} The response to muscle stretch in the colliculus, however, tends to be in the deeper layers, brief, and excitatory¹ rather than in the superficial layers, prolonged, and inhibitory as is the suppression response in our experiments. In addition, the suppression frequently starts close to the time of onset of the eye movement, and although the latency of the response to muscle stretch can be short, only the shortest latency proprioceptive effects could account for the suppression. Finally, since the suppression we observed was associated with eye movements in many directions, and was only slightly modified by a threefold change in eye movement amplitude (Figure 9), it seems unlikely to result from stretch receptors which are sensitive to direction of movement, i. e., which muscle is activated, and size of movement, how much stretch.⁴ These characteristics of the suppression in the colliculus would seem to make proprioception an unlikely source for the effect. Additional experiments are required to determine definitively the roles of proprioception and mechanical shearing in the suppression in the colliculus.

We think the most likely source of the extraretinal input to the superior colliculus is a corollary discharge from some part of the oculomotor system. Cells discharging in relation to eye movement in other parts of the nervous

system are possible candidates for this corollary discharge. Cells in the intermediate layers of the superior colliculus lie adjacent to the visual neurons we have studied, and these cells discharge with eye movements in light and darkness but precede the eye movement,^{46,50,51,59,60} and therefore, the timing of their burst seems inappropriate to generate the extraretinal signal (Figure 14).

An area that has an established projection to the superior colliculus as determined by Nauta degeneration methods³ is the frontal eye fields. This area of cortex has been shown by Bizzi^{9,10} to contain cells which discharge after eye movements. Experiments by Mohler et al.⁴¹ confirmed these observations, and an analysis of their data shows that the timing of the discharge of these cells largely overlaps the suppression in the superficial layers (Figure 14). These neurons discharge after eye movements to large parts of the ipsilateral and contralateral visual field so that they could easily generate the poor directionality of the suppression in collicular cells. In addition, Guitton and Mandl³¹ have found that stimulation of the frontal eye fields of the cat can reduce visual responses of collicular cells. Thus, in terms of timing, directionality, anatomical connections, and physiological effects following stimulation, the frontal eye fields appear to be an ideal candidate for the source of a corollary discharge, as was originally suggested by Bizzi.⁹ However, since our knowledge of the activity of cells in many areas of the brain in relation to eye movements is limited, and since the colliculus receives afferents from a wide variety of areas,²⁸ it would be premature to identify one area as anything more than a potential source for the input.

Comparison of superior colliculus and striate cortex. Cells in the superior colliculus show a clear differentiation between external stimulus movement and image movement which results from an eye movement. Furthermore, the mechanism of this differentiation appears to be a threshold elevation timed to occur after the eye movement at just the time that the effects of the visual stimulus arrive in the colliculus. These findings on the colliculus are in striking

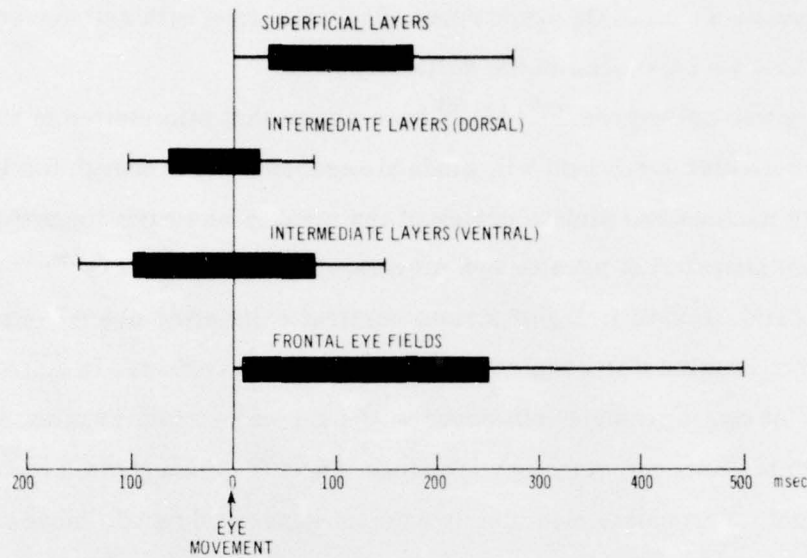


Figure 14. Relation of timing of extraretinal signal to the timing of several possible sources of the signal. Ends of thin bars indicate ranges; ends of thick bars show averages. Top bar shows duration of suppression seen in superficial layer cells following spontaneous eye movements made in total darkness (data from 19 neurons derived from Figure 10). Second bar shows timing of discharge of the most dorsal intermediate layer cells recorded in a penetration which was at least 0.5 mm long and on which at least two intermediate layer cells were recorded. Third bar shows the timing of the discharge of the most ventral intermediate layer cells from same penetrations. Data for second and third bars are taken from 18 penetrations made in the experiments of Mohler and Wurtz.⁴² Bottom bar gives timing of discharge of frontal eye field neurons in association with eye movements made spontaneously in total darkness. Data are derived from experiments on nine cells by Mohler et al.⁴¹

contrast to the previous observations made on striate cortex using the same techniques to study the same part of the visual field, and in the same laboratory.⁵⁸ In contrast to the colliculus, striate cortex cells did not discriminate between the stimulus movement and eye movement conditions. The visual background was a powerful influence in cortex compared to the apparently slight effect of background in collicular cells. Cortical cells also did not show the

striking suppression of the background discharge rate with eye movements in the dark that we have seen in the colliculus.

Doty and colleagues^{5-7,17,55} have shown that stimulation of the mesencephalic reticular formation will modulate transmission through the lateral geniculate nucleus and striate cortex of the monkey and have suggested that the brain stem stimulation mimics eye movements. Other reports^{19,34} have described a reduction of firing of striate cortical cells after eye movements in the dark, but averaging was required to demonstrate the effect. In spite of these examples of eye movement influences in the geniculostriate system, their functional implications are very unclear since Wurtz⁵⁸ demonstrated that striate cortical cells respond to stimulus movement generated by eye movements. In any case, cortical effects are slight compared to those in colliculus. Thus, superior collicular cells show clear differentiation between stimulus movement and movement produced by a saccadic eye movement while striate cortical cells do not.

Such a dichotomy is not surprising since there are several other differences between these major branches of the visual system. Whereas most cortical cells are fastidious in their feature detection properties,^{5,18,33,56} collicular cells are nonspecific in their stimulus requirements.^{16,29} Furthermore, many cells in the superior colliculus show an enhanced response to a stimulus presented in the vicinity of its receptive field when it is to be the target for a saccadic eye movement.^{30,61} Striate cortical cells show this enhanced response in association with any eye movement.⁶² In sum, cells in the striate cortex are finely tuned for details of visual stimuli and are nonspecifically influenced by eye movements. Collicular cells are very poorly tuned for stimulus features but their visual responses are significantly modified by eye movements.

Functional significance. Interpretations of the functions of the collicular cells which distinguish between the two stimulus movement conditions will be strongly influenced by where the axons of these neurons project. Efferents of the colliculus can be broadly divided into two groups, those ascending to thalamic

nuclei such as the pulvinar and those descending to brain stem nuclei, such as the mesencephalic and pontine reticular formations, and interstitial nucleus of Cajal.^{8, 43}

If the information encoded in these cells ascends to the thalamus and then to the cortex, we are inclined to think of a perceptual function for the effect. Humans (see review by Martin³⁶) and monkeys⁴⁰ have an elevation of threshold for the detection of stationary flashes of light beginning just before and extending until after a saccadic eye movement, termed a saccadic suppression.

While part of this elevation probably results from a background masking effect produced by the sweep of the visual field across the retina during an eye movement, a fraction of the effect is due to central processes.⁴⁵ Although the time courses of the behavioral and electrophysiological suppressions are similar, if allowance is made for conduction time of the visual stimulation effects, the amount of threshold elevation demonstrated for saccadic suppression is slight, usually 0.5 log units;⁴⁵ in our experiments we studied only effects of at least 1.0 log units and frequently the effect was even more striking. There is some indication that detection of moving stimuli may be suppressed more completely during a saccade,¹² and the possibility of decreased sensitivity particularly for movement by collicular cells parallels this psychophysical observation. Thus, it is possible that activity in the superior colliculus contributes to saccadic suppression, although the magnitude of the effect in the colliculus seems greater than necessary to produce the usually slight psychophysical effect on stationary stimuli.

Another perceptual function for an extraretinal signal is the recalibration of visual space.³⁷ Whenever the eyes change position, objects in the visual world excite a different set of retinal receptors; in spite of this, we perceive no change in the position of such objects in visual space. Thus, there might logically be some correction of the visual information to take into account the direction and extent of each eye movement. Collicular cells, by themselves, seem inappropriate for this function. The cells that differentiate between the

two types of stimulus movement are very poorly directional and would seem to provide inadequate information for any such spatial recalibration.

If the effect of this differentiation between real and self-induced movement is directed toward the brain stem, we would expect the effect to be primarily useful to the oculomotor system. For the oculomotor system these cells would provide an uncontaminated signal; the stimulus movement detected would result from movement in the environment and not simply reafference due to the last saccadic eye movement. For cells sensitive to rapid stimulus movement, by far the most frequent source of potential stimulation must be the sweep of the visual world during the ever-occurring saccadic eye movements. By essentially filtering out this stimulation, the system can be made more sensitive to movement in the environment and more useful for initiating saccades to objects that are moving and would possibly be threatening to the survival of the animal.

It has been suggested that the colliculus is involved in the selection of salient features in the visual environment and the facilitation of eye movements toward them.^{28,30,42,61} Two of the mechanisms which would be involved in these processes are the enhanced response to a visual stimulus when it is to be the target for a saccadic eye movement and the elimination of the effects of stimulus movement caused by eye movements. We have found that some collicular cells have both processes. Thus, the superior colliculus is especially well-organized to identify saliency since it has processes for facilitating the effects of significant stimuli and suppressing the effects of erroneous ones.

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