

Organization of Monkey Superior Colliculus: Enhanced Visual Response of Superficial Layer Cells

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SUMMARY AND CONCLUSIONS

1. Cells in the superficial layers of monkey superior colliculus respond more vigorously to a spot of light falling in their receptive fields when the monkey uses that spot of light as the target for a saccadic eye movement. Our purpose in these experiments was to investigate the characteristics of this enhancement effect. While monkeys fixated, we determined the response of a cell to a stimulus falling in its receptive field. Then we determined the response of the cell to the same stimulus when the monkey made a saccade to the stimulus or near to it.

2. The enhancement of the visual response is spatially limited. The receptive field of a cell always shows enhancement throughout its extent and frequently shows a slight expansion. Saccades made near to a stimulus in the visual receptive field, but not to it, also lead to an enhancement of that visual stimulus; an area around the excitatory center of the receptive field where such enhancement occurs was referred to as the enhancement field of the cell. An enhanced response in one part of the visual field was not accompanied by depressed responses associated with saccades to other parts of the visual field.

3. The enhancement effect is temporally limited; it begins 200–300 ms before the eye movement, as determined by the increasing response to 50-ms light pulses presented at varying intervals before the eye movement. The degree of enhancement intensifies when the visual stimulus is turned on closer in time to the onset of the saccade. A buildup of the enhancement also occurs on successive trials as does the response of eye movement-related cells in the intermediate layers.

4. The enhancement response is not present in the upper quarter-millimeter of the superficial

layers, suggesting that the effect is not present in retinal afferents which terminate primarily in this area of the superficial layers. The enhancement effect is seen throughout the visual field; the foveal area was not tested.

5. In order to determine the relation of the enhancement effect to the monkey's behavioral response, we required the monkey to make a hand response rather than an eye movement-response to the visual stimuli. Cells did not show a clear enhancement with such a hand response. Results of these experiments indicate that the enhancement effect is dependent on the type of response the monkey makes to the stimulus and is probably specifically related to eye movements. Since the enhancement of visual response seems likely to be related specifically to eye movements both on physiological and behavioral grounds, the response-free term "attention" is probably inappropriate for the phenomenon.

6. The hypothesis advanced in the preceding paper that eye movement-related activity from intermediate and deep colliculus layers is directed upward to converge with visually related activity in the superficial layers is extended to include an input from cells in these deeper layers (or their afferents) to the superficial layer cells. The characteristics of the visual enhancement can be almost entirely accounted for by assuming such an input from the deeper movement cells.

INTRODUCTION

Many cells in the superficial layers of the monkey superior colliculus respond more vigorously to a spot of light falling in their receptive field when the monkey uses that spot of light as the target for a saccadic eye movement (5). This enhanced response to the visual stimulus results from the monkey's use of the stimulus and not a change in the stimulus itself.

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Furthermore, the response enhancement is selective; the response of the cell to a visual stimulus occurs when the monkey makes a saccade to that stimulus, but not when the monkey makes a saccade to a stimulus distant from the receptive field. This selectivity led Goldberg and Wurtz (5) to suggest that these cells in the superior colliculus may be part of a neural mechanism underlying the behavioral phenomenon of selective attention.

The purpose of this paper is to investigate the characteristics of this enhancement effect. Experiments consider: 1) the spatial extent of the enhancement effect within the visual field, 2) the temporal course of the enhancement, 3) the organization of cells showing the enhancement within the colliculus, 4) the relation of enhancement to the type of behavioral response made to the stimulus. The results of these experiments suggest that the enhancement phenomenon may be explained by extending the hypothesis of an upward flow of eye movement information developed in the preceding paper. This interpretation of the enhancement effect also clarifies and limits the relation of the enhancement effect to the psychological phenomenon of selective visual attention.

A brief report on several of these experiments has been published previously (24).

METHODS

These experiments used the same behavioral task described in the preceding paper (12) in which the monkey fixated on a point of light on a tangent screen 57 cm in front of him. During the time the monkey looked at the fixation point, it was possible to stimulate one area of the retina repeatedly by projecting another spot of light onto the screen and to thereby determine the receptive field of the cell. This receptive-field stimulus came on 0.5 s after the fixation point came on and stayed on for the duration of the trial. The timing of events in this fixation task is shown schematically in Fig. 1A. The background illumination of the tangent screen was 1.0 cd/m^2 and the stimuli (produced by quartz-iodide and tungsten slide-projector lamps) were 1.0–1.5 log units above background. The most frequently used visual stimuli were $0.25^\circ \times 0.25^\circ$ to $1^\circ \times 1^\circ$ squares of light.

After learning this basic fixation task, each monkey was trained on one or two additional tasks shown schematically in Fig. 1B and C. For the eye-response task (Fig. 1B), the monkey depressed the bar to turn on the fixation point. But now, as the receptive-field stimulus came on (0.5 s after the fixation point appeared), the fixation point went off. The mon-

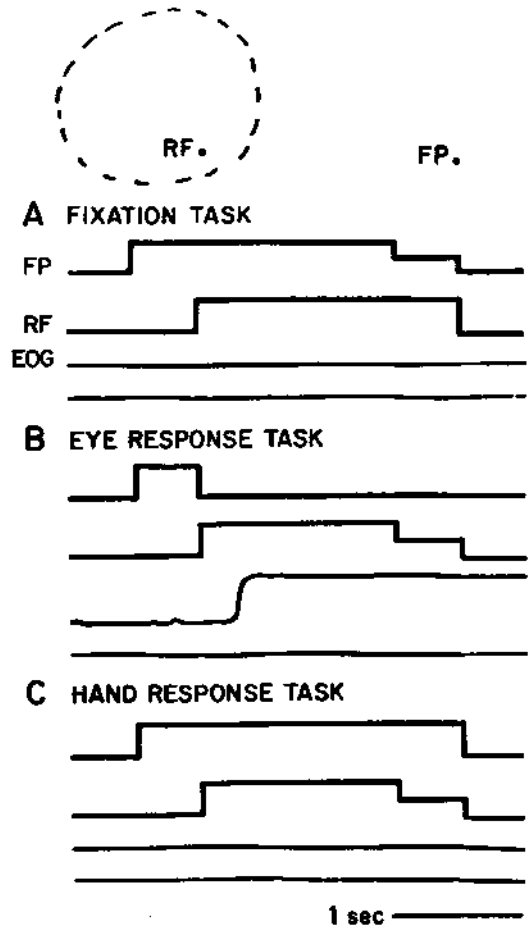


FIG. 1. Schematic drawing of paradigm for fixation task (A), eye-response task (B), and hand-response task (C). In A, the monkey responded to the dimming of the fixation point. In B the monkey responded to the receptive-field stimulus by making a saccadic eye movement to it, while in C the monkey made no eye movement to the stimulus but instead responded with its hand when the stimulus changed. Drawing at top shows a hypothetical receptive-field outline (dotted line circle) with a receptive-field stimulus (RF) at one point; FP is the fixation point. See section on behavioral methods for details.

key learned to make a saccadic eye movement to the receptive-field stimulus (as indicated by the electrooculogram records), fixate on it, and release the bar when this stimulus dimmed; this is the same task used previously by Goldberg and Wurtz (4). On some trials the receptive-field stimulus did not dim, but instead, the stimulus went off and the fixation point came on again and dimmed. This variation minimized the advantage to the monkey of fixating on the receptive-field stimulus and simply waiting for it

to dim. This eye-response task was used in the following experimental sequence as a cell was studied: 1) The visual receptive field of the cell was mapped while the monkey was fixating (the outline of a hypothetical receptive field is shown by dotted lines near the fixation point, FP, in the drawing of Fig. 1). 2) The consistency of response of a cell to a visual receptive field stimulus (RF in the drawing in Fig. 1) was determined over a number of trials while the monkey was fixating. 3) The monkey then made saccadic eye movements on successive trials from the fixation point to the visual receptive-field stimulus and the response of the cell was again determined. Because of the monkey's reaction time to make a saccadic eye movement, there was approximately 200 ms from the time the visual stimulus came on to the time when the eyes began to move from the fixation point. The visual stimulus activated the neuron as in the fixation task during this 200 ms. In the eye-response task the monkey used the stimulus as a target for a saccadic eye movement; in the fixation task there was no behavioral response dependent on the stimulus. The visual stimulation of the receptive field was the same in the fixation and eye movement segments of this task; only the significance and behavioral response to this stimulus was changed.

In order to determine the effect of a saccade to points outside the visual receptive field of a cell, a modification of the eye-response task was also used. In this variation of the task both the receptive-field stimulus and an alternative saccade target came on when the fixation point went off. The monkey learned to make the eye movement to the target not on the receptive field because it was this target that might now dim rather than the receptive-field stimulus.

The third task, the hand-response task (Fig. 1C) required that the monkey release the bar in response to a change in the visual receptive-field stimulus rather than make an eye movement to it. As in both the fixation task and the eye-response task, the visual receptive-field stimulus came on 0.5 s after the fixation point. In this task, 1-3 s later, either the fixation point or the visual stimulus dimmed in a random fashion, and the monkey obtained his reward by releasing the bar when either dim occurred. Since the tiny fixation point continued to dim randomly on half the trials, the monkey was required to continue to fixate on this point. If his eye position changed by more than 2° after the visual stimulus came on, the trial was automatically terminated by the computer. But, since the receptive-field stimulus also dimmed on the other half of the trials, the monkey was

forced to respond to this stimulus and thereby indicate his use of the stimulus. The hand-response task was used in the following experimental sequence: 1) the visual receptive field of the cell was mapped while the monkey was fixating, 2) one point in the visual receptive field was repeatedly stimulated in a series of trials and the consistency of the response of the cell determined while he was fixating and responding to the dimming of the fixation point, 3) the response of the cell was recorded while the monkey responded with a hand movement (bar release) to the dimming of either the visual stimulus or fixation point while maintaining fixation. Since there was no difference in the visual stimulus in the fixation and hand-response tasks, any difference in response of the cell to the visual stimulus during these tasks must result from a change in the significance of the stimulus, i.e., the monkey could ignore the visual stimulus in the fixation task, but had to respond to changes in the visual stimulus in the hand-response task.

It is conceivable that the monkey could adopt a strategy of attending to both the fixation point and the receptive-field stimulus in the hand-response task described above. Although this would be a difficult way to solve the fixation trials, the result of such a strategy could be an equivalent response of the cell in the fixation and receptive-field dim trials. In order to force the monkey to respond to stimuli in a part of the visual field remote from the receptive field of a cell, we utilized a variation of the hand-response task. In this variation the monkey depressed the bar and the fixation point appeared, but now two visual stimuli appeared 0.5 s later. After a variable interval of 1-3 s, either the fixation point dimmed or one of the visual stimuli dimmed. The monkey was required to maintain fixation as in the standard hand-response task. For this variation of the hand-response task, one of the visual stimuli was placed on the visual receptive field of the neuron under study and the other placed contralateral to the receptive field. The response of each neuron was studied during the following sequences: 1) The response to the two visual stimuli was measured while the monkey was fixating. 2) The response of the cell was determined when either the fixation point or the visual stimulus on the receptive field dimmed in random fashion. 3) The discharge of the cell was determined when either the fixation point or the visual stimulus contralateral to the receptive field dimmed. The visual stimulation was the same throughout the sequence. In the first condition, the monkey made no motor response dependent on the two visual stimuli. In the sec-

ond case, the monkey made a hand movement which was triggered by the visual receptive-field stimulus. In the third case, the monkey made a hand movement which was triggered by a visual stimulus that was distant from the receptive field of the stimulus.

For convenience we will refer to the two tasks in Fig. 1*B* and *C* as the eye-response task and the hand-response task. We should emphasize, however, that these names refer to the first response the monkey makes to the stimulus, but in both tasks the monkey eventually responds with a release of the bar, that is, a hand response.

Eight monkeys were used in these experiments, but we concentrated on different tasks and procedures in the experiments on different animals. Four monkeys were used on the eye-response task, one on the hand-response task, and one on both eye-response and hand-response tasks. A few experiments were also done on cells in the superior colliculus in two monkeys which had partial lesions of the striate cortex contralateral to the colliculus studied. Experiments done on these two monkeys were repeated and the results confirmed on the other normal animals, and none of the data from these two monkeys is included in the population statistics presented.

Recording procedures and experimental programming were identical to that described in the preceding paper (12).

RESULTS

We studied the effect of the eye-response task on 300 cells in six monkeys. These cells gave on responses to small spots of light anywhere within the central area of their receptive fields, frequently had clear inhibitory surrounds, and were similar in all respects to cells previously referred to as "pandirectional" cells (4), which were shown by histological verification to lie in the superficial layers of the superior colliculus (stratum zonale, stratum griseum, and stratum opticum). The latency of the on-response for different cells ranged between 35 and 60 ms (a slightly wider range than reported previously by Goldberg and Wurtz (4)), but for most cells the latency was between 40 and 50 ms.

Of these superficial layer cells, 40% gave an enhanced response when the monkey used a stimulus in the visual receptive field of the cell as the target for a saccade (using the eye-response paradigm shown in Fig. 1*B*). Figure 2 shows an example of such enhancement. The displays in the left column are rasters in which cell discharges are represented by dots and suc-

cessive trials by successive lines. The vertical line indicates the time of the stimulus onset. The histograms in the right column represent the summation of the rasters. Figure 2*A* shows the response of the cell to the spot of light projected onto the receptive field while the monkey looked at the fixation point (no-saccade condition). Figure 2*B* shows the response of the cell to the spot of light when the monkey made saccadic eye movements to the spot of light (saccade condition). The density of cell discharges in the initial on-response is increased in Fig. 2*B* as compared to Fig. 2*A*, and this will be referred to as early enhancement. The drop in frequency of discharge about 300 ms after stimulus onset in Fig. 2*B* results from the removal of the spot of light from the receptive field due to the eye movements which begin 200–250 ms after stimulation. Other cells have both the increased on-response and a more prolonged period of increased cell discharge, which will be referred to as a late response enhancement (see ref 5). About half of the cells showing an enhanced response had an early or an early and late response enhancement; the remaining cells had only a later response enhancement.

As reported previously (5), the enhancement effect is selective; it occurs only with eye movement made to the receptive field but not away from the receptive field. For example, in Fig. 2*C*, both the receptive-field stimulus (RF) and a control spot of light (CON) outside the receptive field came on when the fixation point (FP) went off.¹ On these trials the monkey made a saccade to the control point since now only the control spot was dimming, and no comparable enhancement of the response to the visual stimulus is evident. On other cells a slight enhancement of the response developed with saccades to the control stimulus, but the effect was always slight compared to the enhancement seen with saccades made to the receptive-field stimulus.

Spatial characteristics of enhancement effect

We first investigated the effect of saccades made to different points within the receptive field on the spatial organization of the receptive field. We determined the response to a spot of light at each point in the field in the no-saccade (fixation) condition and then in the saccade

¹ Note that in this experiment the stimulus configuration in Fig. 2*C* is different from that in Fig. 2*B* since the control stimulus is not present in 2*B*. Experiments with identical stimulus conditions have been reported previously (ref 5, Fig. 5).

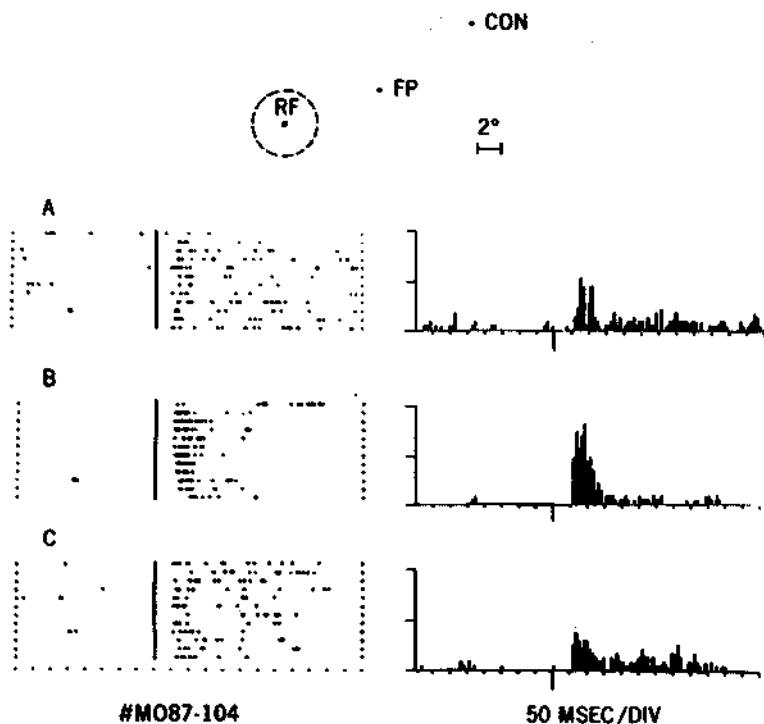


FIG. 2. Selective enhancement of the on-response of a cell to the receptive-field stimulus. On this and subsequent figures, histograms on the right are constructed from the same cell discharges as displayed in rasters. On histograms in this and following figures, the bin width is 8 ms and the vertical scale indicates the height of a bin if a cell discharged at 250 spikes/s per trial. Stimulus onset is indicated by the vertical line below the histogram. Time between dots along the abscissa on both rasters and histograms is 50 ms. Trials in *A* show the cell discharge to the receptive-field stimulus (RF in the schematic drawing—the circle indicates the excitatory central region of the receptive field) while the monkey was looking at the fixation point (FP). In *B* the increased response is associated with saccades made to the receptive-field stimulus. In *C* the monkey made saccades to the control stimulus (CON) in the contralateral visual field (as determined from EOG records) and no enhancement occurred.

condition. The upper segment of Fig. 3 (labeled fixation) shows the histograms for the visual response at points in and surrounding the visual receptive field of a cell mapped in the no-saccade condition. There is a clear gradient of response to the spot of light with a peak at a centrally located point and a sharper decrease of response toward the fixation point than away from it. The lower segment of Fig. 3 (labeled saccade) shows the responses at each point when the monkey used that point as the target for a saccade. The enhancement of response occurs at all points within the receptive field including the central points, which were already responding vigorously in the no-saccade condition. At the fringe of the receptive field some points which did not respond in the no-saccade condition now show a response to the visual stimulus. Note that the new points appear where the gradient of response from point to point is slight; the point closest to the fixation

point, where the response gradient is steep, shows no response during either the no-saccade or the saccade condition. The inclusion of a usually subliminal fringe around the edge of the receptive field during the saccade condition could result from a reduction in an inhibitory surround process or a potentiation of the excitatory central process, but we have no evidence to distinguish between these possible mechanisms. In 16 experiments in which we were able to study enough points to determine if expansion of the receptive field occurred, 11 cells showed a comparable slight expansion. In all cases the spatial organization of the receptive field was largely unchanged; the enhanced response extended nearly equally throughout the field and sometimes expanded the field slightly in the area away from central vision.

Our next question was whether a saccade directly to the receptive-field stimulus was required or whether a saccade anywhere in the

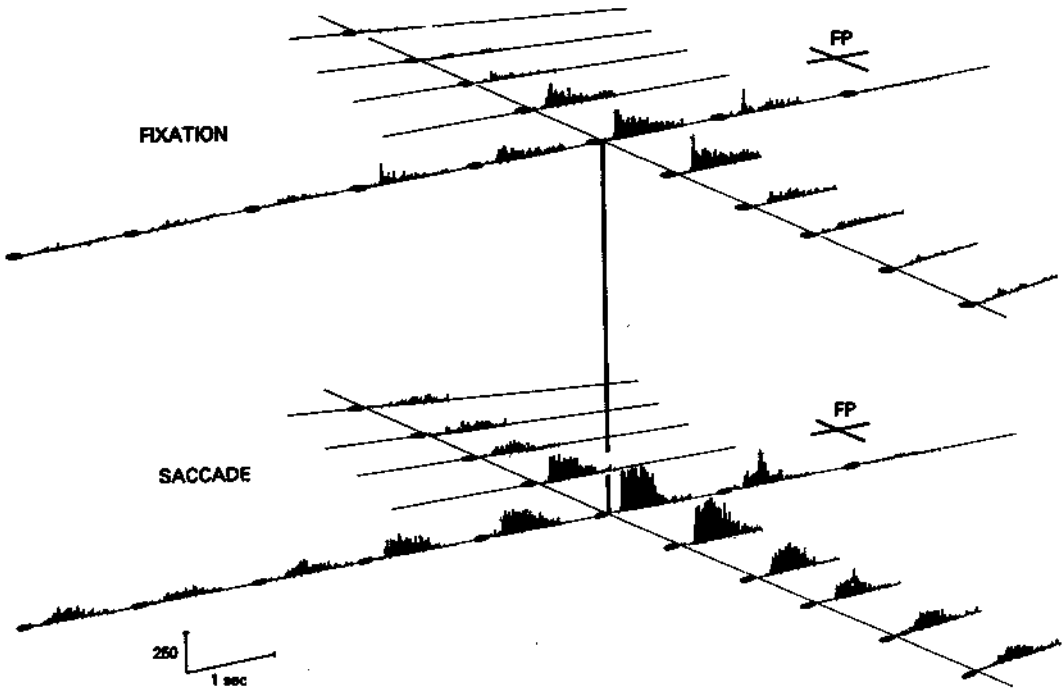


FIG. 3. Gradient of the visual response throughout the receptive field of a superior colliculus neuron. Top field was determined while the monkey fixated and bottom while the monkey made saccades to the visual stimulus. Each filled circle represents the location of a spot of light as it is plotted on a horizontal projection plane. Distance between points is 2.5° ; FP indicates the location of the fixation point. Histograms were obtained from 12 stimulus presentations. The time of stimulus onset is indicated by the filled circle; the histogram is 1 s in duration, bin width is 8 ms, and the vertical scale in the lower right corner indicates the height of a bin for a cell discharging at 250 spikes/s on each stimulus presentation. The vertical line between the two planes connects the central point in each plane for ease of comparison. The cell response is enhanced at all points throughout the receptive field in the bottom plane including points on the receptive-field fringe which did not respond at all to visual stimulation in the no-saccade condition.

vicinity of the receptive-field stimulus was adequate to produce the enhancement. To answer this question we used the same basic paradigm as in Fig. 2C. Both the receptive-field stimulus and another spot of light (the saccade target) came on as the fixation point went off and the monkey made a saccade to the target; on successive blocks of trials this spot of light was moved farther from the receptive-field stimulus. Figure 4A shows the response of the cell to the receptive-field stimulus (dark square) and a saccade target A close to it when the monkey was fixating (Fig. 4A1) and when he was making saccades (Fig. 4A2); a clear early and late enhancement is evident in the saccade condition. When the saccade target was moved so that it came on at point B and the receptive-field stimulus came on as before, there was also an enhanced visual response in the saccade condition (Fig. 4B2 compared to 4B1). We conclude from this and similar experiments that the saccade target can be a point other than the

receptive-field stimulus and still lead to an enhanced response to the receptive-field stimulus.

We found, however, that while the target point did not need to be the same as the visual receptive-field stimulus, the target point had to be close to the receptive field to produce an enhanced visual response. For example, in Fig. 5 the central excitatory region of the receptive field (outlined by the solid line) was first mapped by stationary spots of light. Then the target point was moved to various points in the visual field, and the response of the cell to the receptive field stimulus (and possibly the target point) was determined in the no-saccade and saccade conditions as in Fig. 4. Enhancement of the visual response was clear for saccades made to points close to the receptive field (target spots marked with a plus in Fig. 5) and not at points more remote from the field (spots marked with a circle in Fig. 5). In general, there was a gradation of effect: saccade targets closer to the receptive-field stimulus were associated with

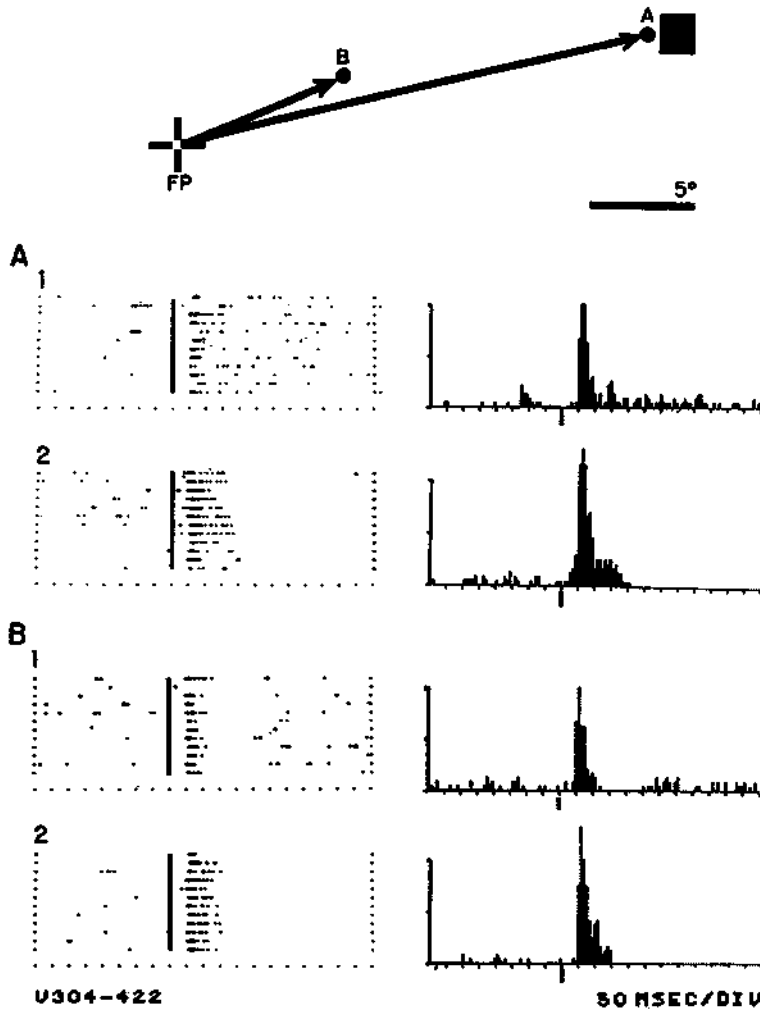
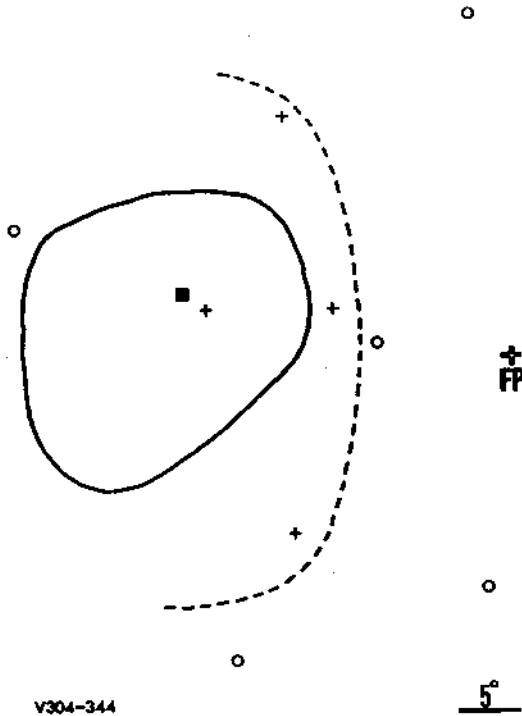


FIG. 4. Enhancement of the visual response with saccades made to points other than the receptive-field stimulus. In the schematic drawing the square indicates the receptive-field stimulus; dots, the saccade targets at point A or point B. Rasters and histograms show the visual response following onset of the visual stimulus and the spot at point A when the monkey was fixating (A1) and when he was making saccades to point A (A2). Records in B show the response when the same visual stimulus and the spot at B came on during fixation (B1) and during saccades to point B. Even with the saccade target outside the receptive field (at point B), some enhancement in the visual response is apparent.

greater enhancement of response to the visual stimulus than points more remote from the field. In addition, this experiment indicates that saccades to target points clearly outside the excitatory response area of the receptive field can lead to an enhanced response. This area is enclosed as far as the experimental results permit with a dashed line in Fig. 5 and might reasonably be called the "enhancement field" of the cell as opposed to its visual receptive field. The enhancement field described in Fig. 5 was generally larger than the enlargement of the visual

responsive area seen in the experiments such as that in Fig. 3.

We also determined whether an enhanced response to visual stimuli in one area of the visual field entailed a decrease in response to visual stimuli in other parts of the field. For 26 cells (12 showing enhancement when a saccade was made to the receptive-field area, 14 showing no such enhancement) we had the monkey make saccades to some point remote from the visual receptive field as the visual stimulus came on in the receptive field. No clear reduction of the



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FIG. 5. Example of enhancement field which is larger than the excitatory central area of the visual receptive field. Solid line outlines area in which 1° spots of light gave an excitatory response. Square indicates site of visual stimulus, while +'s and o's indicate location of saccade targets. Slight enhancement was obtained at saccade targets marked +; no enhancement at target marked o. Dashed line outlines the medial edge of the expanded area where saccade targets which were not in the visual receptive field led to an enhanced visual response.

visual response below the no-saccade level occurred (see Figs. 2C and 4B for examples). In the monkey colliculus response enhancement above the normal no-saccade level in one area of the visual field was not accompanied by a depression of the response to stimuli falling in other parts of the visual field.

This question of the interrelations between different parts of the visual field was particularly important because recent studies in the cat superior colliculus indicate that a moving stimulus remote from the mapped receptive field of a cell reduces the response of the cell to a spot of light within the receptive field (15). We thought this effect might be related to the paralyzed cat's intention to move its eyes to the remote stimulus. In experiments on six cells we moved the second stimulus which was remote from the receptive field (with no saccade used at all) to try to test in the monkey the observa-

tions made on the cat; no reduction in response was observed.

In summary, these experiments show that the spatial organization of the receptive field of colliculus cells is only slightly altered by the enhancement effect. In addition, the area of the visual field over which such enhancement extends is limited to a region around the saccade target; saccades made to other parts of the visual field only minimally alter the discharge of the cell.

Temporal course of enhancement effect

The enhancement effect in different cells consistently shows a graded effect ranging from early enhancement through early and late enhancement to late enhancement only. Our next experiment attempted to bring this variation in enhancement under experimental control. First, we found that we could convert a late enhancement to an early enhancement. For example, in Fig. 6A the response was clearly enhanced in the saccade condition (Fig. 6A2) as compared to the no-saccade condition (Fig. 6A1), and the enhancement was nearly entirely in the later response beyond the initial on-response. In Fig. 6A2 the fixation point went off at the same time the receptive-field stimulus came on, but in Fig. 6A3 this timing was modified. Now the fixation point went off (the signal to make a saccade) 150 ms before the receptive-field stimulus came on. The monkey made a saccade with about the usual latency after the fixation point went off so that the saccade occurred just after the onset of the visual receptive-field stimulus (see sample eye trace above Fig. 6A3), and the enhancement was now clearly an early one rather than a late one. It is possible that the late enhancement was still present, but at this time the eye movement had moved the visual stimulus off the receptive field. When a cell gave a predominantly early enhancement, this enhancement could be increased by forcing the monkey to start the process of making the saccade earlier (Fig. 6B). These experiments (on six cells) show that the early and late enhancement responses can be shifted back and forth in time by shifting the temporal relationship between the monkey's saccade and the visual stimulus.

We tested further 13 cells which showed no enhancement in the standard eye-response task. We had the monkey make a saccade just after the visual stimulus came on in an attempt to produce an enhanced response where there was none before. No enhancement appeared in these cells. The cells which show the enhancement seem to be a fraction of the cells within the colliculus, and this fraction has not been

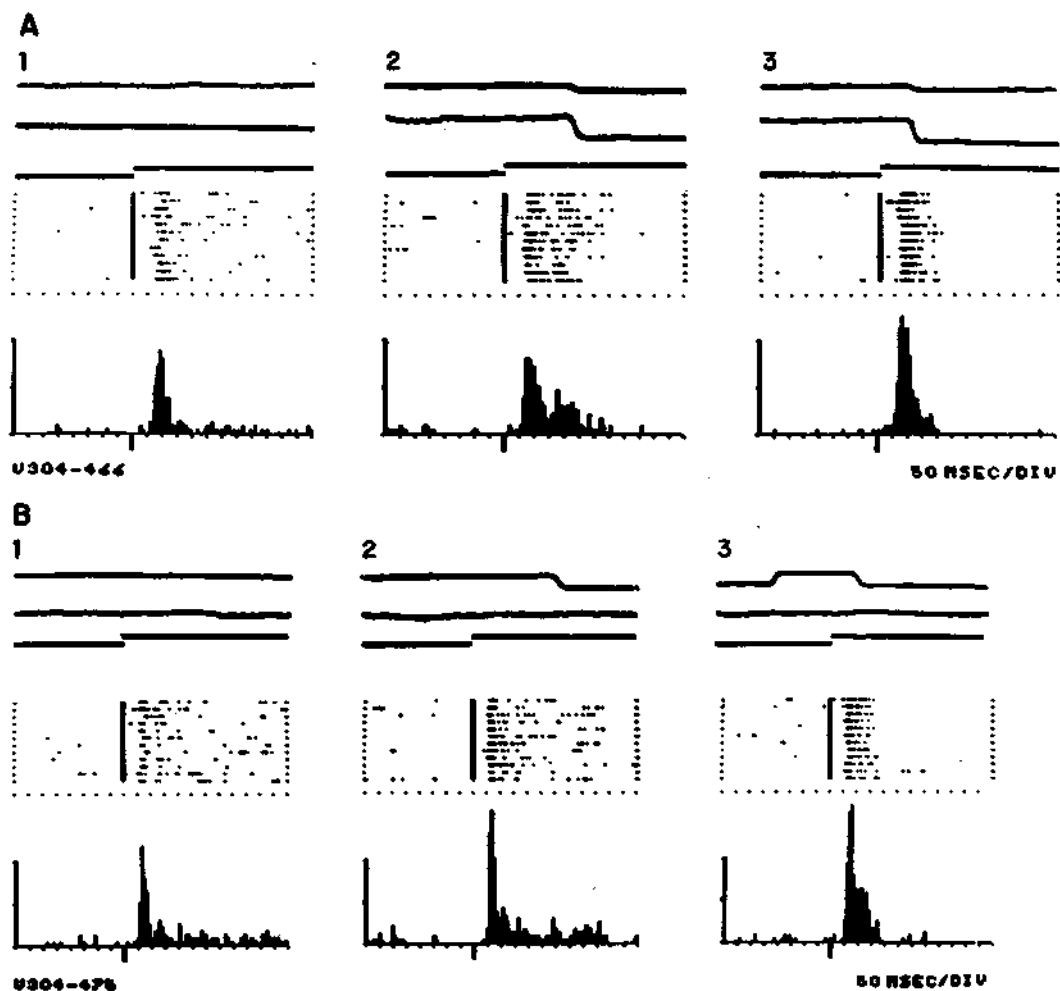


FIG. 6. Conversion of late enhancement to early enhancement by forcing an earlier saccade to the visual stimulus (A) and potentiation of early enhancement by an early saccade to the visual stimulus (B). In 1 of each section the visual stimulus came on during fixation trials. In 2 the fixation point went off as the visual stimulus (which is also the saccade target) came on, the monkey made a saccade to the visual stimulus, and a slight late enhancement is evident in A2 or a slight early enhancement in B2. In 3 the fixation point went off before the visual stimulus came on (100 ms in A3, 150 ms in B3); the monkey made an earlier saccade and there is now a clearer enhancement of the early response.

changed by any manipulation we have discovered.

Having seen that the type of enhancement could be modified, we tried to determine the overall time course of the enhancement effect on three cells. Instead of using a continuous receptive-field stimulus, we tested the responsiveness of a cell with a 50-ms flash of light given at different times before the eye movement. We used a small spot in the receptive field as the saccade target and also turned on a receptive-field stimulus for 50 ms at times progressively closer to the eye movement. Figure 7A shows the visual response to this stimulus

while the monkey was fixating, and Fig. 7B shows that no visual enhancement is present for the stimulus 300–400 ms before saccade onset. By 200 ms before the saccade there is a late enhancement (Fig. 7C), and by 50 ms before the saccade there is an enhancement of the on-response (Fig. 7D). The enhancement effect therefore begins between 200–300 ms before the saccade for this cell. The process underlying the enhancement is, therefore, a phasic one; it is not present as the fixation trial starts, but builds up closer to the time of occurrence of the eye movement.

We also tested responsiveness of enhance-

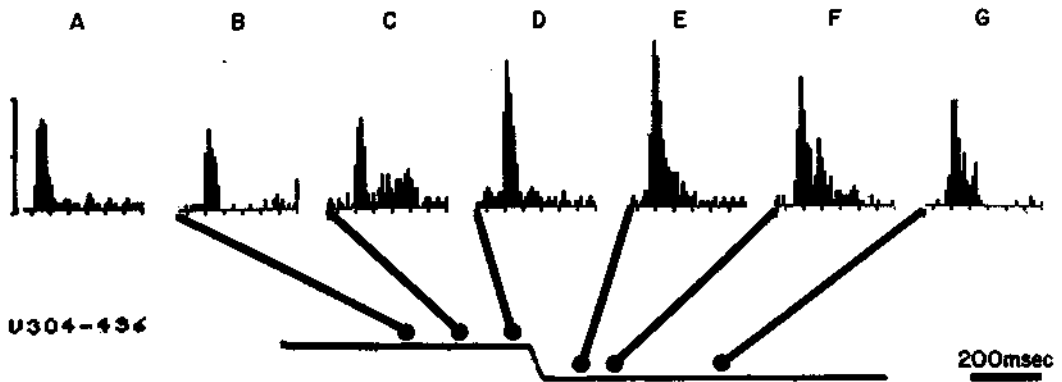


FIG. 7. Time course of the enhanced visual response. Histograms show the response to a 50 ms duration visual stimulus flashed at the times shown by dots above the eye movement trace. In *A* the 50-ms flash was presented while the monkey fixated. In *B*, *C*, and *D* the stimulus was presented a given time before the signal to make the saccade (fixation point off) so that the time before the actual saccade is variable; this variation is small since the monkey was making saccades with a regular latency which averaged about 200 ms. In *E*, *F*, and *G* the visual stimulus was triggered by the end of the eye movement. No enhancement is present when the stimulus precedes the eye movement by more than 300–400 ms (*B*). The enhancement effect begins with a late enhancement effect at *C*, and rises to a peak at *D*. This enhancement effect continues after the eye movement, as indicated particularly in *E*.

ment cells after the eye movement on two cells. For this experiment the monkeys made a saccade to the initial fixation point that was equal in amplitude to a saccade from the fixation point to the saccade target. At the completion of this saccade, the eye movement-recognition program triggered the projection of the 50-ms stimulus onto the receptive field. There was clear enhancement just after the eye movement (as in Fig. 7*E*) in both cells which disappeared by 500 ms after the saccade (as in Fig. 7*G*). While these few experiments indicate that the enhancement effect is present after the eye movement ends, we have not done enough experiments to determine either the frequency of this enhancement or its time course.

A buildup of the response enhancement also occurred from trial to trial so that the second and third response on which the monkey used the stimulus as a saccade target generally showed more enhancement than the first response. Figure 8 shows this effect by comparing the enhancement of the visual response seen on a series of sequential saccade trials (Fig. 8*B*) with the enhancement seen on a raster where each line is the first saccade trial from a series of saccade trials (Fig. 8*C*). Some late enhancement is evident in this collection of first saccade trials, but nothing as marked as the overall enhancement on continuous trials. This increase in enhancement on a continuous series of saccade trials is similar to the increased response of eye movement cells during sequential saccade trials (Fig. 11 of ref 12).

This buildup of response enhancement over several trials is similar to the buildup seen in movement-related cells in the intermediate layers of the colliculus when the monkey makes repeated predictable saccades to the same target (12). For example, Fig. 9*A* shows the development of an enhanced visual response on several trials after the signal to start making saccades was given on the fourth trial. Figure 9*B* shows the same sequence of events as in Fig. 9*A*, but for an eye movement cell. The monkey started making saccades on the fourth trial and the lead of the cell discharge gradually increased until it actually preceded the onset of the trigger signal.

These experiments on the time course of the enhancement indicate that the effect develops on each trial. In addition, the buildup of enhancement from trial to trial parallels a similar anticipatory buildup of rate of discharge in the movement cells of the deeper layers which was described in the preceding paper (12).

Enhancement and collicular organization

We have had the impression that cells showing the enhancement phenomenon occurred more frequently as the electrode was advanced deeper into the colliculus, but since we usually advance and retract the electrode in small steps it was difficult to be sure of this point. To determine the relation of frequency of enhancement to depth of cells in the superficial layers, we made all of the penetrations in one monkey by advancing the electrode only downward; we

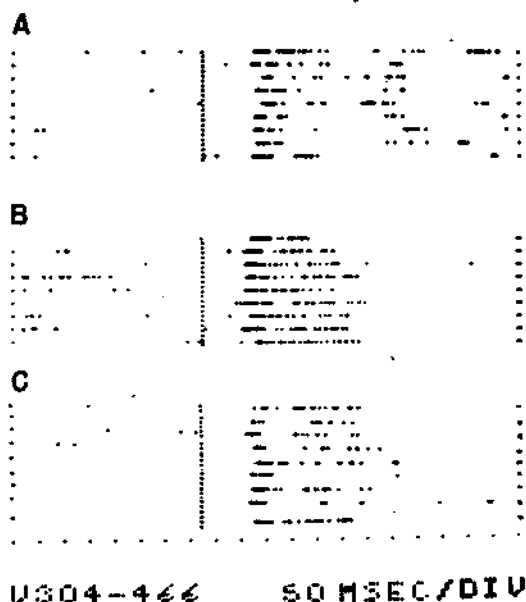


FIG. 8. Comparison of enhancement on successive saccade trials with enhancement on the first saccade trial of each series. In *A* the monkey was fixating and the trials were continuous one after the other. In *B* the trials were also continuous but the monkey was making saccades to the receptive-field stimulus. In *C* the monkey is making saccades, but each line is the first saccade trial of a series and the trials are therefore discontinuous.

did 16 penetrations on which three or more cells were studied. In the graph of Fig. 10, the frequency of enhancement found in these penetrations is plotted against the depth of the cell in the colliculus. None of the first visual cells isolated showed enhancement, and only one of nine cells in the first quarter-millimeter below

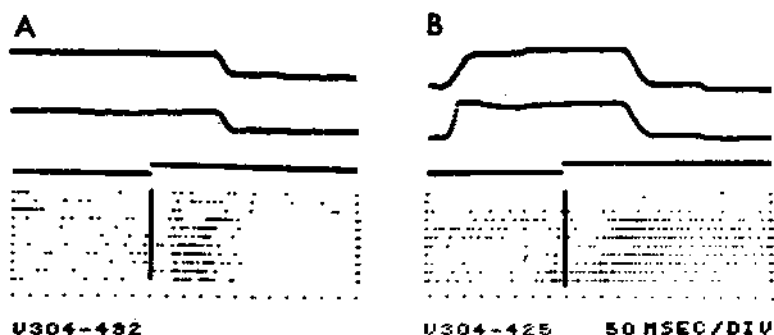


FIG. 9. Development of the enhancement effect over successive trials in visual cells in the superficial layers (*A*) and the movement response in intermediate layer cells (*B*). In *A*, the monkey was fixating for the first three trials and then making saccades to the visual stimulus on subsequent trials. The enhancement became clearer over the first several saccade trials. In *B*, the monkey also fixated on the first three trials and then made saccades to a target on subsequent trials. The response occurred with a shorter latency after the visual trigger on successive trials and anticipated the visual trigger on the last two trials.

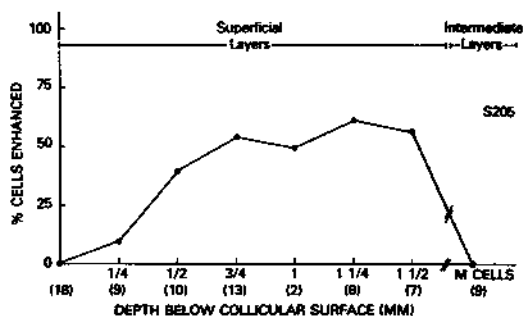


FIG. 10. Changes in frequency of response enhancement with depth of cells in superior colliculus. The zero point is the dorsal surface of the colliculus which was taken as that point where visually activated multiple cell activity was clearly detected. Data are from 16 penetrations in which the electrode was only advanced downward and 3 or more cells were encountered on the penetration. Resolution of the microdrive scale was 0.25 mm; numbers below each depth on the abscissa are the number of cells recorded at that depth. M cells on abscissa refer to eye movement-related cells which also had visual receptive fields. Penetrations entering the colliculus at an oblique angle would have only slight errors in the depth relationship in the first 0.25 mm, but could have considerably greater errors at deeper points. Enhancement was more frequent in cells found below the first 0.25 mm from the top and absent in the visual response of movement cells (labeled M cells) deep in the superficial layers.

the surface showed the enhancement. Frequency of enhancement increased to about 50% by a depth of 0.75 mm and stayed at about that level with increased depth in the visually related superficial layers. The type of enhancement, early or late, showed no relation to depth of the cell in the colliculus. Instead there was a slight tendency for all cells in a penetration to

show enhancement or no enhancement, but as seen in the last section these relations may be related to variations in the monkey's anticipatory behavior rather than the penetrations per se.

We measured the frequency of enhancement in a total of 133 cells from two monkeys (including the cells of Fig. 10) against distance of the receptive-field center of the cells from the fixation point. The frequency of the enhancement effect is nearly the same in all parts of the visual field and is not concentrated either near the fovea or in the far periphery. No evaluation of areas less than 0.5° from the fixation point has been made since the experimental paradigm we use required identification of the saccade to the receptive-field stimulus on each trial and small eye movements less than 0.5° are difficult to identify with certainty in the EOG.

We also measured the relationship between the latency of the visual response of the cells and their position within the colliculus. Cells showed no consistent variation in visual latency as a function of receptive-field distance from the fovea. With depth in the colliculus, however, there was a tendency for the latency to increase. The increase was slight, usually in the range of 10–20 ms difference between the most dorsal and the deepest visual cell (Fig. 11); however, the increase was consistent for all the penetrations from two monkeys. This increase

in latency coupled with the increasing receptive-field size with depth (4, 7) is consistent with the downward and convergence models of serial processing in the superficial collicular layers (12).

Response specificity of enhancement effect

In order to see the relation of the enhancement effect to the monkey's behavioral response, we required the monkey to make a hand response rather than an eye movement response to the visual stimuli. We studied 55 cells from two monkeys while the monkey was required to release the bar when the receptive-field stimulus dimmed, as outlined in the hand-response task shown in Fig. 1C. An attempted eye movement during the fixation period in these experiments terminated the trial. None of these cells showed any dramatic enhancement while the monkey responded to the stimulus. The response of a few cells (9 of the 55 cells) was slightly enhanced, but this was no more than the slight increase in response associated with eye movements to any point of the visual field (5).

A possible explanation for this lack of enhancement with the hand response was that the cells studied were simply not sampled from the subpopulation of collicular cells that show the enhancement in the eye-response task. We

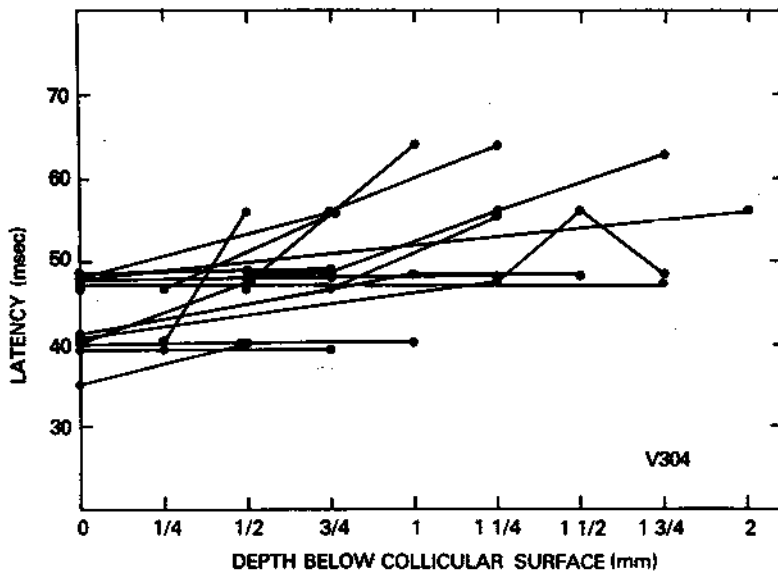


FIG. 11. Change in latency of the visual response with depth below collicular surface. Zero depth was the point at which visually driven multiunit activity was first recorded; subsequent depths were read from microdrive and may not represent penetrations normal to the surface of the colliculus. Latency was determined from histograms with 8-ms bin width or from rasters such as those in Fig. 2. Latency increases slightly with increasing depth.

therefore trained one of the two monkeys to do the hand-response task and to do the eye-response task as well. We succeeded in studying the hand task on 15 cells which showed an enhanced response on the eye-response task; none of these cells showed any clear enhancement on the hand-response task. For example, in Fig. 12 the late enhancement in the eye-response task (upper half of Fig. 12) is clear if *A* (no-saccade condition) and *B* (saccade condition) are compared. But there is little change in the response in the hand task if *A* (only fixation point dims), and *B* (fixation point or receptive-field stimulus dims) are compared.

This lack of enhancement could be due to a number of experimental variables, some of which we could control. One possible problem is that the monkey might have developed a strategy of attending to both the fixation point and the receptive-field stimulus all the time; an enhancement of response would then not show up when the monkey responded to the receptive-field stimulus because he had already been

utilizing the receptive field stimulus throughout the fixation trials. To reduce this effect, we only counted as a valid experiment those series of trials in which the monkey did not respond to the dim of the receptive-field stimulus on the first trial, but did make correct responses to subsequent receptive-field dims. Such improved performance on subsequent trials was taken as an indicator of increased awareness or use of the stimulus. In addition, in some experiments we used not one but two stimuli in addition to the fixation point; one in the receptive field and the other contralateral to the receptive field. We required the monkey to respond to a dimming of the stimulus in the contralateral field over a series of trials in order to shift the monkey's use to that stimulus. We then required a response to the dimming of the receptive-field stimulus. No more striking response enhancement emerged in either of these experiments.

It is possible that there was a different cell response for fixation-point dim trials and hand-response trials when the monkey made a cor-

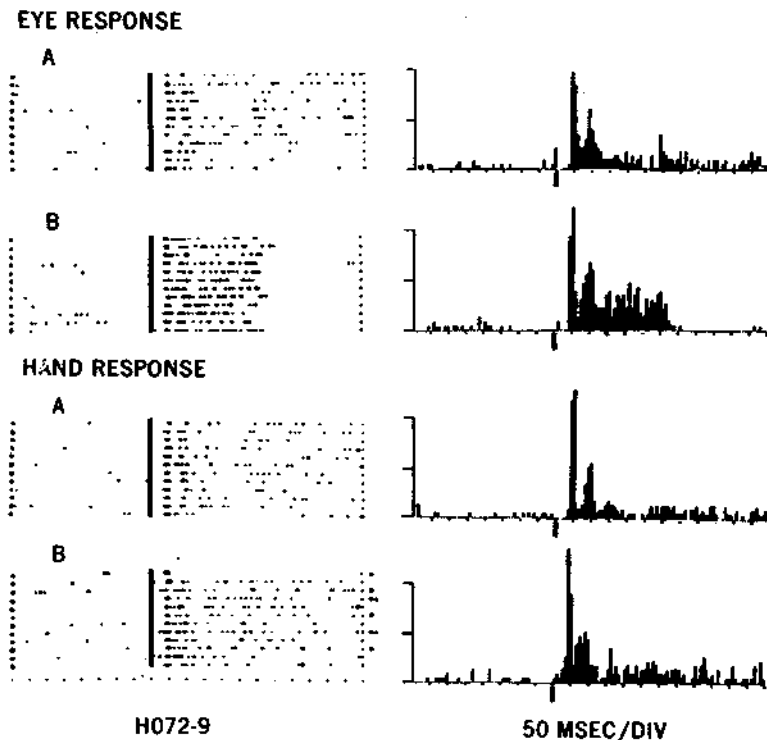


FIG. 12. Lack of enhancement of response when the monkey responds to the stimulus with a hand movement rather than an eye movement. In *A* the monkey is not making saccades (upper segment) or responding to any stimulus change (lower segment). In *B* the monkey is making saccades to the stimulus (upper segment) or responding with a hand movement to a dimming of the stimulus or the fixation point (lower segment). Dots at end of the raster lines in *B* of the lower half indicate trials where the receptive field dimmed (first dot) and on which of these trials the monkey responded correctly to the dim (second dot). Receptive field is about 7° from fixation point.

rect response to the dim of the receptive-field stimulus, but that this enhancement was not visible in the series of mixed fixation-point dim and receptive-field dim trials (as in Fig. 12B). In Fig. 13 the receptive-field dim trials on which the monkey was rewarded are gathered together to emphasize any such enhancement effect. Comparison of the rasters and histograms in Fig. 13A shows that there is a late enhancement in the eye-response task. In Fig. 13B the upper raster and histograms show the response of the cell during a series of fixation trials while the lower ones show a group of nonsequential trials on which the receptive-field stimulus dimmed and the monkey responded correctly. Comparison of these two rasters and histograms shows no clear enhancement.

Another possible problem in comparing the results of the eye- and hand-response tasks was that in the eye-movement task, the enhancement associated with first saccade trials is frequently minimal (Fig. 9) and many of the trials in the hand-response tasks might be regarded as first trials, and therefore not be expected to show a dramatic enhancement. This, however, would not apply to trials with consecutive hand-responses to the visual stimulus (as in Fig. 12B). In addition, this argument assumes that

the monkey is not ready to respond to the stimulus dim on other trials, an assumption we cannot verify or reject in these experiments.

Finally it should be noted that the hand-response task requires only a release of the bar rather than an immediate response to one point in space as in the eye-response task. A more analogous hand-response experiment would require the monkey to continue to fixate while reaching for the target point, a task sufficiently unnatural and difficult to produce apprehension on the part of the experimenter and disbelief on the part of the monkey.

Subject to the above limitations, these experiments indicate that the enhancement effect is dependent on the type of response the monkey makes to the visual stimulus; it is present during the time the monkey makes saccades to the stimulus, but it is not when the monkey responds only with a hand movement to a change in the visual stimulus.

Comparison of visual cells with enhancement to visually triggered movement cells

The cells of the superficial layers showing the visual enhancement effect do not give a burst of

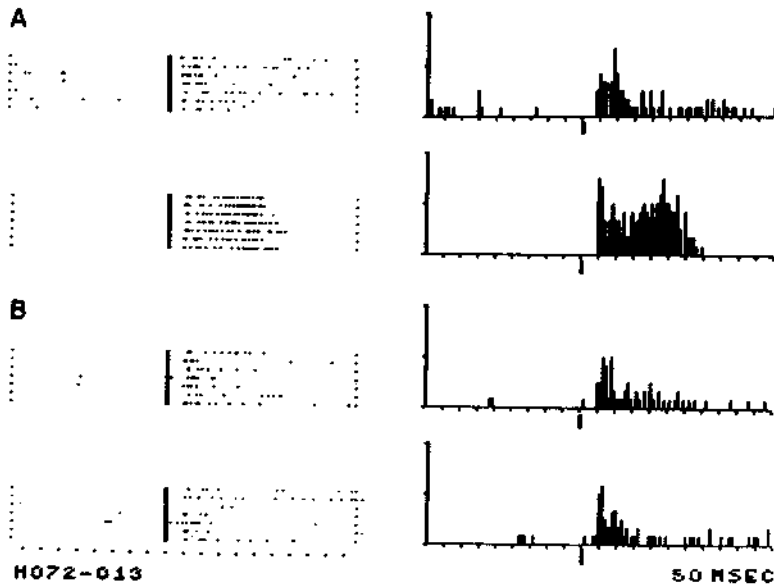


FIG. 13. Comparison of cell discharge to a receptive-field stimulus in the eye-response task (upper segment) and the hand-response task (lower segment). In the upper raster and histogram of A the monkey is fixating, and in the lower raster and histogram of A the monkey is making a saccadic eye movement to the receptive-field stimulus. In the upper raster and histogram of B the monkey is not responding to the receptive-field stimulus, and the lower raster and histogram of B are nonsequential trials where the monkey responded correctly to the dimming of the receptive-field stimulus. Notice that there is an enhancement of the visual response on the saccade trials in A, but there is no enhanced response on trials where the monkey responded to the receptive-field dim with a hand response.

discharge preceding a spontaneous eye movement made in the light or dark as do cells in the deeper layers of the colliculus (4, 21, 22). The enhancement, therefore, represents a modulation of the visual response, not simply a discharge in association with eye movement (4). The visually triggered movement cells which were considered in the previous paper (12) are similar to the visual cells showing enhancement in that they do not give a burst of discharge before spontaneous eye movements. Both types also respond to visual stimuli when no eye movement is made (Fig. 14A1 and B1), but the two types differ in the temporal relation of their discharge to eye movements (Fig. 14A2 and B2). The enhanced response of the cell shown

in Fig. 14A2 is a continuation of the original visual response while the visually triggered eye movement cell shown in Fig. 14B2 responds with a short burst about 50 ms after the visual target comes on (as in Fig. 14B1) and with a second eye movement burst 190–370 ms after visual target onset. The variable onset of the second burst is due to the variable latency between visual stimulus onset and saccade onset, as shown when the response raster is lined up on saccade onset (Fig. 14B3). The enhanced response of the visual cell (Fig. 14A3) is not temporally locked to the eye movement. Figure 14A4 and B4 show that neither of these cells give a burst of discharges before spontaneous saccades made in the dark.

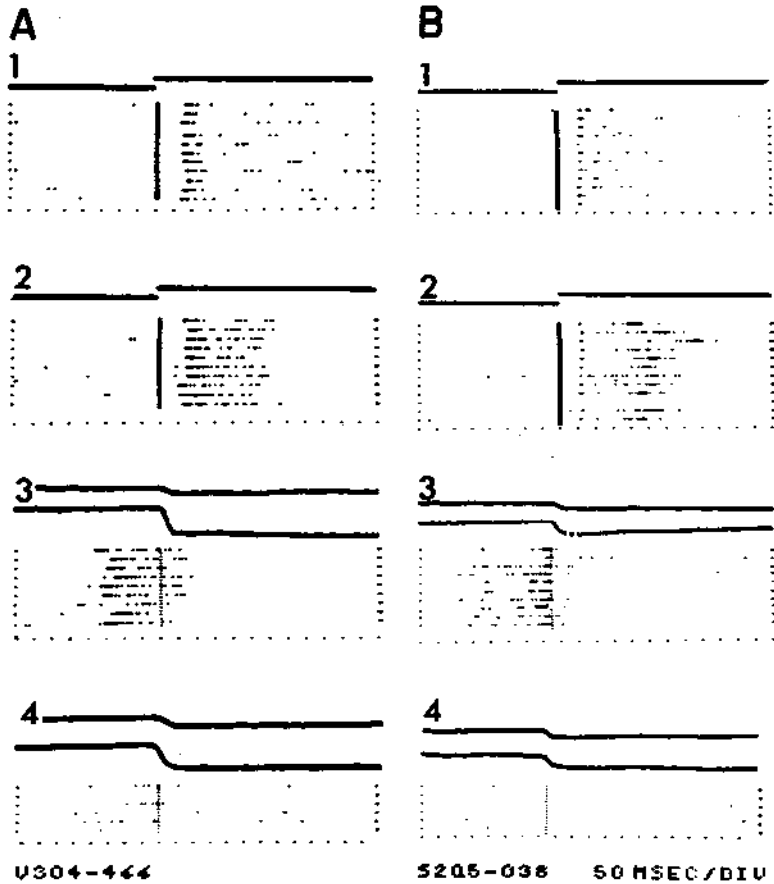


FIG. 14. Comparison of a visual cell whose visual response is enhanced when the visual stimulus is used as a saccade target (A) to a visually triggered movement cell (B). In 1 in each section the rasters are lined up on the onset of a visual stimulus and no saccade is made. In 2 the raster is also lined up on the visual stimulus which was also the target for a saccade. In 3 the trials in which the monkey was making saccades to the visual target are lined up on the onset of the eye movement. Note that the late burst is well synchronized with the eye movement for the visually triggered eye movement cell (B) but that the prolonged increase of the visual response is not so well synchronized for the visual cell (A). In 4 the rasters are lined up on the onset of a spontaneous saccade in darkness of the same amplitude as in parts 2 and 3, but there is no response for either of these cell types.

Both of these cell types show an increased rate of discharge when the monkey makes a saccade to a visual target. The operational distinction between them is that the increased discharge rate is temporally locked to stimulus onset for the visual cells and more temporally locked to the eye movement for the visually triggered movement cells. We should note, however, that the cells in Fig. 14 were selected to emphasize the differences between these two cell types. We find cells where it is much more difficult to distinguish the two cell classifications. For example, if the cell in Fig. 14B2 had a more tonic visual response before the final burst, it would be much more difficult to classify. We think that these two cell types probably represent the ends of a continuum of collicular cells whose visual excitability is altered in association with saccades. On one end of the continuum the cells have a strong visual response which is enhanced before visually triggered saccades (enhancement cells). At the other end of the continuum, the cells have a weak visual response but a burst of cell discharges that is increased before visually triggered saccades (visually triggered movement cells).

DISCUSSION

These experiments have demonstrated four salient characteristics of the enhancement effect. First, the enhancement of the visual response is spatially limited: it is selectively related to the area of the visual field surrounding the saccade target. The saccade target need not be the same as the visual target, but the two must be close together. Second, the enhancement effect is temporally limited: it begins 200–300 ms before the eye movement. Third, the enhancement effect is absent in the top 0.25 mm of the superficial layers. Fourth, the enhancement effect is related to the type of response made to the stimulus and possibly specifically related to an eye-movement response. On the basis of these observations we can now consider three points: the origin of the enhancement effect, the relation of the enhancement to selective visual attention, and the implications of these experiments for understanding the functions of the superior colliculus.

Eye movement-related cells and enhancement effect

The preceding paper (12) suggested that eye movement-related activity in the intermediate and deep layers of the colliculus moves upward, joining with visually related activity moving down through the superficial layers. By extending this hypothesis we think we can explain the

characteristics of the enhancement effect. The extension assumes that some movement-related activity continues into the superficial layers instead of stopping at the junction of the visual and movement cells. In Fig. 15 the chain of shaded arrows moving down and up and joining at the border between superficial and intermediate layers is the same as proposed for the convergence model in the preceding paper. The additions are two solid arrows, one extending from the intermediate layers directly to the superficial layers, and the other extending from the inputs of the movement cells to the superficial layers. Either the movement cells themselves or their afferents could equally well provide the necessary inputs to the visual cells. The requirements of these inputs are only that they have a short latency (but not necessarily a monosynaptic latency) and that they facilitate the responses of the superficial cells without being able by themselves to drive them. As dis-

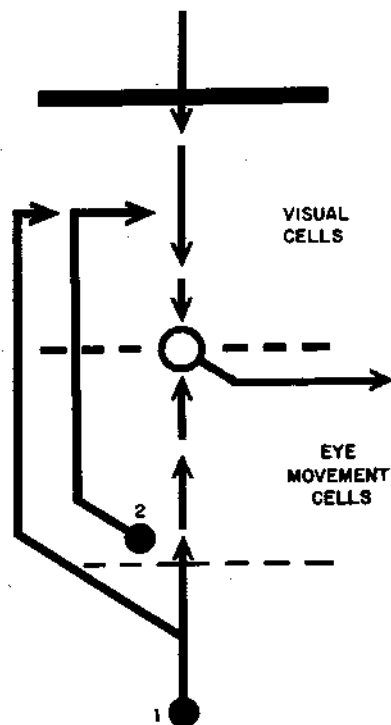


FIG. 15. Model of how the enhancement effect in superficial layer cells could reflect an input from cells deep in the intermediate layers or afferents to these intermediate layer cells. These two inputs are indicated by the solid black arrows. This upward-directed movement activity may be independent of the convergence of the downward-directed visual activity and the upward-directed movement activity (indicated by gray arrows), as proposed in the preceding paper and indicated by the shaded arrows.

cussed in the preceding paper, it should be emphasized that this connection is a matter of conjecture; anatomical and physiological evidence on intracollicular connections is not clear enough to support or reject the hypothesis. What follows is an explanation of the characteristics of the visual enhancement effect assuming that a connection from intermediate layer movement cells or their afferents is present.

The key observation which suggests such an input from movement-related cells is the temporal course of the visual response enhancement. The enhancement effect results from a phasic buildup on each trial (as shown in Fig. 7) rather than a tonic setting of excitability which continues through a series of trials. Therefore, the enhanced effect requires an input to the superficial layers from cells that discharge before an eye movement, which we have found extensively in the intermediate layers, instead of an input to the superficial cells from continuously discharging cells, which we have not found in the deeper collicular layers.

The time course of the enhancement effect before the eye movement matches closely the time course of the deeper movement cells. The enhanced response to a stimulus begins roughly 200 ms before onset of a saccade (Fig. 7), and allowing for a response latency of 35–60 ms after onset of the stimulus, the increase in collicular cell excitability begins 140–165 ms before the eye movement, and increases to near peak levels at the time of saccade onset. This is consistent with the timing of the deeper eye movement cells whose discharge frequency begins to increase rapidly 125–150 ms before saccades (Figs. 2 and 3 in the preceding paper (12)) and rises to peak frequency roughly at the time of saccadic onset. In addition, the discharge of the movement cells can actually anticipate the stimulus trigger in a series of trials, and in this case the movement-related discharge can precede saccade onset by an even longer time. This anticipatory discharge of movement cells can easily account for an enhancement effect as early as 300 ms before the eye movement. However, it is clear that the enhancement effect would require an input from the deeper long-lead eye movement cells, and so the arrows in Fig. 15 are drawn from the deeper part of the colliculus or its afferents.

The persistence of the enhancement after the eye movement, as seen in Fig. 7, is consistent with the continuous discharge of the eye movement cells after the eye movement, but is of longer duration than is seen in the eye movement cells. This postsaccade excitability change might result from an input other than

the eye movement cells. Since we have done the postsaccadic enhancement experiment on very few cells and know little about its characteristics, we can not now evaluate it any further.

That late enhancement can be shifted to early enhancement by inducing an earlier eye movement (as in Fig. 6), is also understandable if a movement cell input is responsible for the effect. For an earlier saccade the discharge of the intermediate cells begins earlier so the input to the superficial cells would also come earlier. In this case the intermediate layer input does not prolong the visual response as in the late enhancement, but potentiates the on-response for an early enhancement. Since the early and late enhancement could therefore reflect the monkey's readiness to make an eye movement, it is not surprising that the early and late enhancement effects bear no relationship to depth in the colliculus.

The enhancement of the on-response to the visual stimulus seems at first difficult to explain by an eye movement-related discharge that is presumably initiated by the visual stimulus itself. That presumption, however, is wrong; cells in the intermediate layers can actually discharge in anticipation of the visual stimulus triggering a saccade when the trigger is given regularly in a series of trials. This anticipatory discharge occurs before the visual stimulus comes on and is, therefore, early enough to facilitate the on-response of the superficial cells to the stimulus. The buildup of the visual enhancement, particularly on the on-response, over several consecutive trials follows along with the observed development of an anticipatory discharge of the deeper movement-related cells over several trials (cf. Fig. 9). If anticipation is eliminated, the enhancement effect is reduced (Fig. 8), and under the same experimental conditions the movement-related discharge is also reduced (Fig. 11 in ref 12). The persistence of the enhancement effect when the monkey is no longer making saccades to the visual stimulus (5) is consistent with the observation that the movement cells can also discharge at the appropriate time even though no eye movement is made (Fig. 12 of the preceding paper).

In summary, the temporal characteristics of the enhancement before the eye movement could be accounted for by the time course of discharge and the anticipatory characteristics of the deeper movement-related cells.

The spatial characteristics of the enhancement effect are also consistent with the organization of the movement fields of the deeper colliculus cells, but the comparison is considerably

more qualitative. If the enhancement results from a facilitation of the visual cells by the movement cells, the area of the visual field over which this facilitation occurs should be influenced by the movement fields of the deeper cells. All indications are that the movement fields (the portion of the visual field where a saccade into the area is preceded by a burst of cell discharges) of intermediate cells are in the same general part of the visual field as are the visual receptive fields of the visual cells just above (17, 22). Therefore, movement cells deeper in the colliculus could simply project to visual cells above them. Since the movement fields of the deeper eye movement cells are larger than the visual receptive fields (Figs. 5 and 10 of ref 12), the area of influence of an intermediate layer input should be large. A number of characteristics of the enhancement effect fit with this assumption. First, the large enhancement field of the visual cells can be regarded as a reflection of the large movement fields of the intermediate cells. The observation that the visual enhancement is present even when the eye movement is not directed to the visual stimulus itself (Figs. 4 and 5) is also readily explained; the enhancement will depend on whether the eye movement is within the movement field of the cell deep in the colliculus, not whether the eye movement is in the visual field of the superficial layer cell. Second, the fairly equal enhancement throughout the visual field is understandable since the gradient of response throughout the movement fields (17) is very gradual so that the effect on a visual field would be expected to be about the same throughout. Third, the slight expansion of the visual field might result from the facilitation by a larger movement field of a subliminal fringe in the visual field.

In net, the spatial characteristics of the visual enhancement effect are easily explained by assuming they are derived from the movement fields of the intermediate cells.

An input from the intermediate layer cells or their afferents to the superficial layer cells is more reasonable than several of the other prominent anatomical inputs. The lack of enhancement in the most dorsal 0.25 mm of the superficial layers (Fig. 10) suggests that the effect is not present in the retinal input to the colliculus since this input terminates in the most superficial 0.25 mm of the superficial layers in the monkey (at least from the contralateral eye (6)) and in the cat (20). Also, the striate cortex is not a likely source of the enhancement effect since the selective effect is not present in cells of the striate cortex (24, 25) and removal of striate cortex does not abolish the effect in col-

licular cells ipsilateral to the cortical lesion (25). The visually related cells in the frontal eye fields (11) show an analogous enhancement effect (25) and send a projection to the superior colliculus (primarily to intermediate layers, ref 1 and 9), but these visual cells in frontal eye fields are also an unlikely source for collicular enhancement since they have a longer latency for the visual response (50–120 ms) than do collicular cells (35–60 ms). Therefore, it is improbable that these three major inputs to collicular visual cells are mediating the enhancement effect.

Any input to superficial layers of the colliculus must take into account the fact that these visual cells are organized on a retinal map i.e., they are related to an area of the retina regardless of where the eye is directed (4, 17). Since the enhancement effect is tied to these visual fields (cf. Figs. 3 and 5), the enhancement also is tied to a retinal map. Such a restriction rules out most of the brain stem oculomotor neurons as the source of the input producing collicular enhancement because the response of these cells is not tied to a retinal map; the vigor of the response associated with a given amplitude saccade can vary with the position of the eye in the orbit (for references and discussion see ref 8). In contrast the movement fields of the intermediate layers are not dependent on orbital position. Thus the intermediate layer cells are a possible source of the enhancement effect in the superficial layers while the retina, striate cortex, frontal eye fields, and brain stem oculomotor neurons probably are not.

Finally, the finding that the visual enhancement effect was present in the eye-response task but not the hand-response task (within the experimental limitations considered previously) is also consistent with the hypothesis that deeper collicular cells provide the enhancement input since these deeper cells clearly relate to eye movement. They do not relate to head movement (16), and we see no obvious relationship of these cells to any hand movement in our experiments. In addition since both the visual cells and the eye movement cells are related to a retinal map, it is easy to see how the eye movement-related activity could be superimposed on the visually related activity. On the other hand, a limb movement would probably be based on a real world map since the hand can reach for an object regardless of where the eye is looking, and it is more difficult to conceptualize how to superimpose this real world map on the retinal map.

In summary, these points on the temporal, spatial, anatomical, and response characteris-

tics of the visual enhancement effect can almost entirely be explained by the hypothesis that the movement-related cells in the intermediate layers of the colliculus or their afferents project to the superficial layers. By this hypothesis the readiness to make an eye movement characteristic of the intermediate layer cells is translated into the selective enhancement of the visual response by the connection from intermediate to superficial layers. Whether this hypothesis proves to be correct will depend on the presence of the appropriate anatomical connections and more specific physiological and behavioral tests.

Enhancement, response specificity, and attention

The enhancement phenomena was suggested as a neural correlate of selective attention (5) because the effect modified the visual input when the sensory stimulation remained constant and because the effect was selectively related to eye movements to the part of the field containing the visual stimulus. These observations have been confirmed in the present series of experiments. They indicate, in addition, that the effect might be related to only one type of response, an eye movement. For this reason the question whether the enhancement relates specifically to eye movements or to any use of the stimulus has considerable importance in interpreting the function of the enhancement effect.

Comparison of the results of the eye-response and hand-response tasks suggests that the enhancement is dependent on the type of response made to the stimulus. Furthermore, the physiological evidence summarized above strongly supports the hypothesis that the characteristics of the visual enhancement effect result from an input from the eye movement-related cells in the intermediate layers, and the lack of enhancement in the hand-response task can be viewed as corroborating this physiological evidence. The term attention has usually been used in a way that implies response independence, that is, the modification of sensory input should occur regardless of how the animal responds to the stimulus. Since the enhancement of the visual response appears to be more closely related to a readiness to make an eye movement than to other movements tested, we have avoided using the term selective attention to describe the enhancement effect.

It is possible, however, that at a neural level there might be more than one mechanism for what, at the behavioral level, is referred to as selective attention. For example, for shifting visual fixation there might be one subsystem

for selecting visual targets, and producing eye movements and this system would incorporate a mechanism for selecting inputs from one part of the visual field. In the sense that this system selects (increases the response of cells) to certain visual stimuli, the neural events we have seen would be a correlate of attention. Another system might select certain auditory cues and lead to head movements, and this would be another possible neural correlate of attention. But in both these cases the selection process is related to movement and thus might be more parsimoniously called part of a readiness to respond. This direction of thinking suggests that the global behavioral concept of selective attention might be a composite of many more specific physiological and behavioral fragments, all of which are related to a readiness to respond. In fact, several psychological concepts have been viewed as a preparation for response by Sperry (18) so that viewing attention in this light is hardly novel.

Implications for collicular function

The points considered in this paper and in the preceding one have been primarily directed at an understanding of the internal organization of the superior colliculus. There are several implications, however, relevant to an understanding of the function of the superior colliculus.

From the preceding paper we have seen that the discharge of intermediate layer cells probably does not result from a downward flow from superficial layer cells. Instead, these cells discharge as a result of some other input which already has determined the area of the field to which the eye movement will be directed. The discharge of these intermediate layer cells appears to be closely related to a readiness to make an eye movement. We proposed that this readiness to respond, if it impinges on the superficial layer cells, can account for the enhanced visual response of those cells. Thus the emphasis on stimuli in one part of the field is a consequence of the readiness to respond, which in turn appears to be a characteristic incorporated into the afferents to the intermediate layers. The colliculus, then, is an agent of this readiness and selection process, not the initiator.

These cell types and their organization, therefore, suggest that the colliculus is one stage in the selection of visual targets and in the readiness to make an eye movement to those targets. For example, if a monkey received a cue that an interesting object was in one part of his visual field, these stimulus-selection and readiness-to-respond mechanisms would permit him to rapidly initiate a saccade to a visual

target if it appeared in the anticipated portion of the visual field. This hypothesis that the colliculus can speed up initiation of saccades to a visual target also is consistent with studies which show that after collicular lesions there is a slightly increased latency for initiation of visually triggered saccades (24) and a minor deficit in the accuracy of the saccades (unpublished observations). The finding that the reaction time and accuracy deficits are partial and not complete is consistent with the idea that the colliculus is at a very early stage of eye movement processing (12) and suggests that other inputs are also available to the oculomotor system for initiation and guidance of eye movements.

While we think our observations on the colliculus strongly suggest a selection-of-stimuli and readiness-to-respond role for the colliculus, they do not rule out the widely held "foveation" notion of collicular function. The foveation model proposed that there was a visual-to-motor transition within the colliculus that was the first step in the nuts-and-bolts processing involved in calculating the amplitude of an eye movement (15, 17). As indicated in the preceding paper (12), we think such a transition within the colliculus should be rejected. However, there is no evidence in our experiments to reject the notion that the cells we indicated as a possible output from the colliculus, the visually triggered movement cells, might not themselves

provide visual guidance information. Movement fields are smaller for these cells than for the deeper ones, and although they too lack a sharp response gradient in their movement field, an overlap theory could easily provide position information for the oculomotor system (10). In fact, we know from our own experiments that after recovery from a lesion of the striate cortex the monkey can make fairly accurate saccades and that this guidance is dependent on the integrity of the superior colliculus (unpublished observations). In addition, collicular lesions of the otherwise intact monkey can lead to a higher frequency of double saccades to a visual target, which suggests a slight guidance deficit or a change in strategy (unpublished data). But the extent to which such guidance capability is used in the normal monkey remains unclear.

So far in our consideration of the colliculus we have concentrated on the possible relationship between the colliculus and the initiation of eye movements. But the monkey colliculus has anatomical connections extending upward into the forebrain (2, 13) as well as downward into the brain stem (13). Such ascending collicular output might influence visual processing at other levels of the nervous system including those levels presumably more closely related to perception. The question whether such upward flow of movement-related activity influences processing of visual information in the cerebral cortex is the subject of the following paper.

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