Vision During Saccadic Eye Movements. III.
Visual Interactions in Monkey Superior Colliculus

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SUMMARY AND CONCLUSIONS

1. We investigated whether cells in the superficial layers of the monkey superior colliculus, like those of striate cortex, show effects of visual interaction that might play a functional role in reducing the response of these cells to visual stimulation during saccadic eye movements. We studied these visual interactions while the monkey was fixating in order to eliminate any influence of an additional discharge to the superior colliculus that accompanies saccadic eye movements. We found three types of visual interactions that would reduce the response of a cell to visual stimulation during saccadic eye movements.

2. The first type of interaction resulted from stimulating both center and surround of the visual receptive field with a single stimulus moving at saccadic velocities. A spot of light crossing both the activating center and the suppressive surround produced a weaker response than spots crossing the center alone. Every collicular cell responded to rapidly moving stimuli when the stimuli crossed only the central area of the visual receptive field.

3. The second type of visual interaction was between two stimuli falling within the central area of the receptive field. When a prolonged stimulus (analogous to the stimulus falling on a receptive field before a saccade) preceded a brief stimulus, the response to the brief stimulus was attenuated. No backward effect was observed when a stationary stimulus followed the brief stimulus. These interaction effects were generally similar to those seen in striate cortex. In the superior colliculus the brief stimulus did not need to fall on the same part of the receptive field as the preceding prolonged stimulus for the forward interaction effect to occur. A prolonged stimulus on the opposite side of the receptive field from the brief stimulus still produced attenuation of the response to the brief stimulus.

4. The third type of visual interaction occurred when a brief stimulus falling in the central activating area of the receptive field was preceded by a prolonged stimulus outside the central area. When the prolonged stimulus was placed across the vertical meridian in the opposite hemisphere, a smaller attenuation occurred. The response attenuation by a remote stimulus is similar but not identical to that reported previously in the cat superior colliculus. Our experiments indicate that the effect in the monkey is one involving visual interactions rather than shifts in attention.

5. We found both the visual interaction effects between stimuli and the reduced sensitivity due to a corollary discharge acting on the same cells in the superior colliculus. We suggest that the functional difference between the two mechanisms is that the corollary discharge would be effective over a wide range of light and contrast levels but would only modify the response of about half of the cells in the superior colliculus, while the visual interaction would affect all cells but would work well only when light and contrast levels were relatively high.

INTRODUCTION

Cells in the two visual pathways respond differently to stimuli during saccadic eye
movements, as indicated in the two preceding papers (8, 12). Cells in striate cortex show a clear forward "masking" effect of the prolonged stationary stimulus falling on the receptive field before the eye movement on the brief stimulation during the eye movement. Extravisional input appears to have at most a slight effect on the response of striate cortex cells to stimuli during eye movements (8, 18). In contrast, in the superior colliculus the extravisional input is powerful enough to attenuate the response to stimuli during a saccadic eye movement (15), and the input is the result of a corollary discharge accompanying the saccadic eye movement (12).

The subject of this paper is whether the sensitivity of cells in the superior colliculus is altered during saccadic eye movements, not only by corollary discharge but also by visual masking. We have found that cells in the superior colliculus do indeed show a visual masking effect—an effect we shall refer to as a visual interaction effect since our studies are at the physiological level, not at the psychological level. In addition, we found two other visual factors related to the organization of collicular receptive fields, which must reduce the response of these cells to visual stimulation during saccadic eye movements: the interaction between the activating central area and the nearby suppressive or antagonistic surround and the suppressive effect of stimuli remote from the conventional receptive field.

An abstract of this work has been published previously (11).

**Methods**

The general methods for studying single-cell responses in awake monkeys (Macaca mulatta) while they fixated their gaze or made saccadic eye movements were the same as those described in the preceding two papers (8, 12). The monkeys faced a tangent screen 57 cm in front of them and performed the fixation task (8). While they were fixating, the outline of the activating central area of the receptive field of the cell under study was determined. We studied collicular cells with receptive fields whose centers were between 5 and 25° of the fixation point.

Once we found the outline of the central area of the receptive field, we determined the responsiveness of the cell to either rapidly moving or briefly flashed stimuli. Moving stimuli crossed the most sensitive part of the receptive-field center at 900°s, a velocity comparable to the peak velocity of a 20° saccadic eye movement. The stimuli were usually elongated slits of light (frequently 1° × 3°) moved lengthwise along their long axis (see Fig. 1). The stimuli were 1 log unit above a background of 1.0 cd/m² unless otherwise indicated.

Alternatively, instead of moving the stimulus rapidly across the receptive field of the cell, we simply flashed the stimulus onto the center of the receptive field. The duration of the flashed stimulus was usually 5 ms, a time equal to that of a slit of light moving at 900°s across a 4–5° area of the field. The size and intensity of the flashed stimulus was the same as that of the rapidly moving stimulus.

**Results**

Since many of the visually related cells in the superficial layers of the superior colliculus show a suppression of response following saccadic eye movements in the absence of any visual stimulation (5, 12, 15), we of necessity studied stimulus interaction effects when there were no saccadic eye movements and, thus, no possibility of suppression related to saccadic eye movements. While the monkey fixated, we recorded the response of cells to visual stimuli moved rapidly across the receptive field of the cells or flashed briefly onto the receptive fields of the cells. This procedure allowed us to study the response of cells to the brief stimulation that would occur as a result of saccadic eye movements, but free of the suppression that is a corollary of such eye movements. In three monkeys, we studied 104 cells with visual responses similar to those cells shown previously (4) to be in the superficial layers (superficial gray and optic layers) of the superior colliculus.

**Center-surround interaction**

We found that the response to a visual stimulus by itself was frequently slight when the stimulus swept at saccadic velocity (900°s) across both the central activating area of the visual receptive field and the surrounding suppressive area, but if the stimulus swept only across the center of the field, a stronger response was obtained. While interaction between center and surround is hardly surprising, during saccadic eye movements the interaction becomes important since any saccade is likely to sweep the
image of a contoured environment over both the center and surround of the receptive field. Figure 1 shows an example of the center-surround interaction. When the stimulus swept across both the center and surround, the response was slight (Fig. 1A), but when the stimulus was swept only across the central area of the receptive field, a stronger response was present (Fig. 1B). Reduction of the sweep length even within the central activating area continued to increase the response to the sweep stimulus (Fig. 1C). Every cell in a series of 22 experiments showed the same effect: reduction of the length of the stimulus path to include only the center of the receptive field always produced a more vigorous response. Cells that gave no response when the stimulus swept over the center and surround, and that would have been classified as unresponsive to rapid stimulus movement by Robinson and Wurtz (15), gave a clear response when only the center of the field was exposed or when the stimulus was flashed on the field center. In subsequent experiments using moving stimuli, we swept the stimulus across only the central area of the receptive field in order to maximize the response of the cells.

Since the size of the activating center of the receptive field changes with the depth of the cell in the superficial layers of the superior colliculus (4, 7), it seemed possible that the relative effectiveness of the suppressive surround mechanism on the central activating mechanism might also change with depth. We tested this possibility by record-

FIG. 1. Reduction of response to stimuli moving at saccadic velocity across the suppressive surround of a cell in the superficial layers of the superior colliculus. A shows the response of the cell to a stimulus moving at a velocity comparable to that of a saccadic eye movement (900°/s). The path of the sweep was 20° long centered on the excitatory center of the receptive field. The stimulus was always moving; it did not come on and then move. In B and C the response of the cell was improved by shielding the surrounding areas of the receptive field from the sweep stimulus (without changing the background illumination), as indicated by the shaded areas. In D the stimulus did not move but was simply flashed on for 2 ms (a time comparable to that for the moving stimulus to cover the minimally exposed area in C). In the schematic drawings the stimulus is 5° long, and the central area of the receptive field (shown as a dashed circle) is about 6° in diameter, and the center of the field is about 12° from the fixation point. In this and subsequent figures the cell discharges are indicated as dots, cell responses on successive trials are shown on successive lines, and the histogram is the sum of these lines. Each vertical scale on the histograms is 100 discharges per second per trial, bin width is 6 ms, and the histogram is the sum of eight trials (unless otherwise indicated). The approximate time at which the stimulus crossed the receptive field is indicated by the triangle beneath each histogram. The time scale is 100 ms between successive dots on the time line.
ing multiple-cell responses as we advanced the electrode down through the superficial layers, adjusting the size of the area exposed to the stimulus as the activating region of the receptive fields became larger. We found that the response improved when we swept the stimulus across only the central receptive-field area at all depths of the superficial layers.

When the sweep of the stimulus was confined to just the center of the receptive field, its duration was so brief that its effect was about equal to that of a stimulus flashed briefly on the field, as is illustrated in Fig. 1C and D. When the area of the receptive field exposed to the moving stimulus was the size of the stimulus itself (Fig. 1C), the response of the cell to this moving stimulus was similar to the response to a stimulus not moved but flashed only briefly (5 ms, Fig. 1D). All cells studied (22 cells) showed this stimulus equivalence. We subsequently did many experiments using a flashed rather than a moving stimulus, both because we could then study visual interaction effects in nearly all cells encountered and because the use of a flash enabled us to eliminate any influence of movement on the suppressive surrounds of the receptive field.

From these experiments we conclude that many cells in the superior colliculus may not respond during saccadic eye movements simply because the surround of the receptive field is sufficiently powerful to eliminate the brief stimulation of the center of the field.

**Visual interaction of two stimuli**

We tested the effect of one stimulus on the response of the collicular cells to another stimulus while the monkey fixated. A stimulus came on in the central area of the receptive field for 500 ms and then went off, and 50 ms later a second stimulus swept across the receptive field or was flashed on the receptive field. The first stimulus (the presweep or preflash stimulus, to use the terminology of Judge et al. (Fig. 3 of Ref. 8)), is analogous to a prolonged stimulus falling on a receptive field before a saccadic eye movement, while the second stimulus (the sweep or flash stimulus) is analogous to a brief stimulus falling on the receptive field during an eye movement.

Figure 2 shows the stimulus interaction effects; 2A shows the response of a cell to a sweep stimulus (the triangle indicates the time the stimulus crosses the receptive field), and 2B shows a reduced response when a stationary spot of light (indicated by the black bar) was turned off 50 ms before the sweep stimulus, while 2C shows the response to the stationary spot only. Comparison of the timing of the responses in Fig. 2B and C shows that a substantial part of the remaining response in 2B is the slight off-response to the end of the prolonged stimulus since it is present in 2C when only the prolonged stimulus was present.

We saw a similar forward visual interaction effect when a flashed stimulus of 5 ms duration (Fig. 2D-E) replaced the sweep stimulus. The response to the flash (indicated by the triangle in Fig. 2D) was reduced when it was preceded by a presflash stimulus identical to the presweep stimulus (Fig. 2E). The reduction in the response to the flashed stimulus is clear when the responses shown in Fig. 2E are compared to the responses shown in Fig. 2F when the presflash stimulus was given alone.

The forward effect, that of the presflash or presweep stimulus on the sweep or flash stimulus, was present in all cells tested (58 cells tested with a sweep stimulus, 51 with a flash stimulus—including many cells tested with both stimuli). The magnitude of the effect from cell to cell ranged from a 30 to a 100% reduction in amplitude of the flash or sweep response, as measured by the total number of spikes in the response (see Fig. 4 for details of response calculation). In cells where the response to flash and sweep were both tested, the response to the flash stimulus was usually somewhat more effectively reduced than was the response to the sweep stimulus, as is the case in Fig. 2.

Figure 3A shows the time course of the forward visual interaction for flashed stimuli. When the time between the end of the presflash stimulus and the onset of the flash stimulus was 0 or 50 ms, the attenuation effect on the flash stimulus was maximal. At an interstimulus interval of 200 ms, the attenuation effect on the flash stimulus was still present but much less powerful. Figure 4 shows the time course for seven cells and indicates that this forward effect of the presflash stimulus on the flash stimulus persisted in many cases even at 200 ms. The
FIG. 2. Reduction of response to a sweep stimulus (left column, A–C) or a flash stimulus (right column, D–F) by a presweep or preflash stimulus. A and D show the response to the sweep or flash alone. B and E show the response when each is preceded by a stationary stimulus falling on the receptive field, and C and F show the response to the presweep or preflash stimulus presented alone. Triangles below histograms indicate the time the sweep stimulus or flash stimulus fell on the receptive field. The solid bars below histograms show the presence of the presweep or preflash stimulus—the onset of this stimulus occurs to the left of the edge of the figure so that no on-response is present on the figure. The interval between the presweep or preflash stimulus and the sweep or the flash was 50 ms. The sweep passed over the receptive-field area of the presweep stimulus without crossing the surround; the flash stimulus fell on exactly the same area as the presweep stimulus. The presweep and preflash stimuli were the same size: an 0.5° × 1.0° slit. The stimulus conditions were similar to those in Fig. 1B for the sweep stimulus and Fig. 1D for the flash stimulus. The receptive-field center was 14° from the fixation point and 15° in diameter.

overall time course and magnitude of the forward effect in these superficial layer cells of the superior colliculus appears comparable to that seen for cells in the striate cortex (8).

The effect of a stationary stimulus falling on the receptive-field center after the flash stimulus (a postflash stimulus to continue the terminology of Judge et al. (8)) is illustrated in Fig. 3B. At an interval of 100 ms between the flash stimulus and the postflash stimulus there was little interaction. When the interval was 75 ms, the on-response to the postflash stimulus was reduced, but the response to the flash was not. As the interval between the two stimuli decreased, the amplitude of the postflash stimulus decreased; it was barely detectable at 50 ms, and only one response was present when the two stimuli were simultaneous. More important, there
FIG. 3. Attenuation of response to a flash stimulus by a preflash stimulus (A) and the lack of effect of a postflash stimulus on the flash stimulus (B). Solid bars below each histogram indicate the duration of the pre- and postflash stimuli, and triangles below each histogram indicate the time of the flashed stimulus. The interval between the stimuli (in milliseconds) is to the left of each column. Timing is to the nearest 5 ms so that an interval of 0 means the flash started within 5 ms of onset or offset of the prolonged stimulus, but was not necessarily simultaneous with onset or offset. Stimuli were 2.5° on a side and were superimposed in the central area of the receptive field, which was about 5° from the fixation point and 5° in diameter. In A the response to the flashed stimulus is greatly reduced when the stimulus interval is reduced to 100 ms. The elimination of both the off-response to the preflash stimulus as well as the response to the flash stimulus at short interstimulus intervals (0 and 50 ms) was observed on several other cells, but the on-response to the preflash stimulus usually remained (as in Fig. 2). In B the response to the flash remains unchanged, but the on-response to the postflash stimulus is reduced.
FIG. 4. Asymmetry of time course of forward and backward attenuation effects. The dark line shows the mean and standard deviation for seven cells on the left and four cells on the right. The light lines indicate the response of individual cells. The abscissa is the interval, $\Delta t$, between the preflash and flash stimulus on the left and the flash and postflash stimuli on the right. The ordinate is the difference between the response to the pre- and postflash stimulus alone and the response to the pre- or postflash stimulus when accompanied by the flash stimulus. This was calculated as in the preceding paper of Judge, Wurtz, and Richmond (6): the number, R, of additional spikes generated by presenting the flash stimulus in addition to the preflash stimulus was expressed as a ratio of the mean number of spikes generated by sweep alone, i.e., $R = (M + SW - M) / SW - S$), where $M + SW$ is the number of spikes generated by both stimuli presented together, $M$ the number generated by the mask alone, SW the mean number generated by the sweep alone, and S is the spontaneous count. These numbers were obtained by programming the computer to count and display the number of spikes in a time window set to bracket the interval of the sweep response. In order to cover the whole period of the sweep response we used a window of 50–100 ms. When the flash precedes the postflash stimulus (on the right of the graph), this window width does not allow a distinction between a reduction of the flash response and a reduction of the on-response to the postflash stimulus. The apparent attenuation of the flash response associated with the simultaneous onset of the postflash stimulus, in fact, results entirely from a reduced on-response to the postflash stimulus. These interactions are easily seen in Fig. 3B.

was no backward effect detectable on the flash stimulus at all. Figure 4 shows this lack of backward interaction effect for four other cells. Because of the absence of backward interaction of one stimulus on a preceding one, we concentrated our subsequent experiments exclusively on the forward visual interactions.

To see the time course of the forward effect in the experiments just described, we usually superimposed the flash or sweep stimulus on the preflash or presweep stimulus, just as we did for cells in striate cortex. However, since the central areas of the receptive fields of superior colliculus cells are substantially larger than those of the striate cortex, there might be many occasions when an eye movement would lead to stimulation of one part of the receptive-field center during the saccade, but another part before the saccade. In a short series of experiments (11 cells), we therefore determined whether there was a stimulus interaction if the two stimuli fell on different areas of the receptive-field center.

We first placed the flash stimulus in the center of the receptive field and moved the preflash stimulus to points successively farther away but still within the receptive field. As the distance between the flash and the preflash stimulus increased, the response to the flash increased, that is, the attenuation of the response to the flash was reduced. The decreased attenuation could result either from the increased distance between the preflash and flash stimuli or from a decrease in the vigor of the response to the preflash stimulus as it moved closer to the edge of the receptive field.

We separated the effects of distance and response strength by superimposing the preflash and flash stimuli at a point near the edge of the central activating area of the receptive field, as shown in the receptive-field outline at the top of Fig. 5. Figure 5A shows the magnitude of the response of the
cell to the flash stimulus at different points in the field. As the flash stimulus was placed at the left edge of the receptive field, then moved to the center, and then at the right edge, the response became greater and then decreased, so that the response at the right edge about equaled the response at the left edge of the field. In the stimulus interaction experiment the preflash stimulus remained at position 1, while the flash stimulus moved in subsequent groups of trials from position 1 to position 6. If the distance between the preflash and flash stimulus is important, then the response to the flash stimulus should have increased steadily as the distance between the two stimuli increased. On the other hand, if the relative strength of the responses to the preflash and flash stimuli is important, the response to the flash should have increased as the flash was moved toward the center of the receptive field and then decreased as the flash was moved toward the opposite edge. Figure 5B shows the latter result; the relative response of the two stimuli is most important. In fact, when the flashed stimulus was at one edge of the visual receptive field (position 1) and the preflash stimulus was at the opposite edge (position 6), the response to the flashed stimulus was attenuated just as much as it was when the two stimuli were superimposed at position 1. In other cells, distance between stimuli did have some influence on the stimulus interaction; as distance between preflash and flash stimuli increased, the response attenuation decreased somewhat. But the critical point is that the attenuation effect is present even

![Diagram showing stimulus interaction](image)

**Fig. 5.** Control of stimulus interaction by response strength when preflash and flash stimuli are spatially separated. The schematic drawing shows the position of the flash stimulus in successive blocks of trials. The preflash stimulus always remained at position 1 as indicated by the dark bar. Dashed lines indicate the edge of the central area of the receptive field; width is about 13" and the left edge is about 15" from the fixation point. A shows a bar graph of the response at each point to the flash stimulus alone with the response at position 1 taken as 100%; the amplitude of response indicates the gradient across the receptive field center. B indicates the magnitude of the forward visual interaction effect of the preflash stimulus as the flash stimulus was moved from being superimposed on the preflash stimulus (position 1) to a point on the opposite side of the receptive field (position 6)—see text for further explanation. The magnitude of the response shown on the bar graphs was calculated as described in Fig. 4; each bar was derived from eight stimulus presentations. The interval between the preflash and the flash stimulus was 50 ms.
when the preflesh and flash stimuli do not overlap spatially.

As a further measure of the spatial requirements of the attenuation effect, we replaced the discrete preflesh stimulus with a visual noise pattern in experiments on eight cells. The result was attenuation of the response to the flashed stimulus, although the noise was usually not as effective in reducing the response to the flash stimulus as was a superimposed prefleshe or presweep stimulus. This reinforces the above conclusion that spatial superposition of preflesh and flash stimuli is not necessary for the attenuation of the flash response.

Remote stimulus effects

During the course of the experiments on the spatial separation of stimuli, we noticed that the preflesh stimulus placed out of the central activating region of the visual receptive field still produced a marked attenuation of the response to a flash stimulus within the central area. Such an interaction could, of course, also modify the response of a cell during saccadic eye movements.

This remote stimulus effect is illustrated in Fig. 6. The flash stimulus was always placed in the central activating region of the receptive field (dashed circle in Fig. 6) and the preflesh stimulus either superimposed or placed at the other points shown. While the attenuation of the response to the flash was greatest when the stimuli were superimposed, the response to the flash was still attenuated when the preflesh stimulus produced no response. This attenuation decreased with the distance of the preflesh stimulus from the edge of the excitatory visual receptive field; the attenuation was usually still strong at 20°, and when tested in two cells the effect was still strong at a separation as great as 50° (distance in Fig. 6, left segment is 17°). When the preflesh stimulus was placed across the vertical meridian, the effect was less pronounced and the response of the cell to the flash quickly approached the full response as the
preceding stimulus was moved further across
the vertical meridian (Fig. 6F, right segment).
We have seen some such remote effect
on most cells tested (24 of 28 cells); the
magnitude of the effect was generally com-
parable to that shown in Fig. 6. The amount
of attenuation did not relate to the direction
from the central area of the receptive field
at which we placed the preceding stimulus;
a remote stimulus placed medially from a
lateral field produced the same result as a
remote stimulus placed laterally from a medial
field (as long as the stimuli were on the same
side of the vertical meridian as the receptive
field). In addition, while the interval between
the preflash stimulus and the flash stimulus
was 30 ms in these experiments, variation
of the interstimulus interval showed that the
effect of the peripheral stimulus was present
at intervals between 0 and 100 ms. Longer
time intervals were sometimes effective,
sometimes not. Thus, it is not necessary
for a stimulus to be close to or, in fact,
within the central area of the receptive field
to modify the response to another stimulus
following closely in time, a result similar to
that reported previously in the cat by Riz-
zolatti and his co-workers (13, 14).

Relation of visual interaction
and suppression

We have now found two different factors
that might modify the response of superior
colliculus cells during saccadic eye move-
ments: a suppression effect corollary to sac-
cadic eye movements (5, 12, 13) and the
visual interaction effects shown in the pres-
cent experiments. In order to understand
what relationship might exist between these
two factors, we compared the visual inter-
action effects and the suppression effect on
the same cells in the superior colliculus.

We first checked to see whether the cells
showing the weakest visual interaction ef-
facts between stimuli might be those that
show suppression. Experiments on a series
of cells in which the visual interaction effect
of a flash or sweep stimulus was compared
with the suppression effect showed no such
inverse relationship: cells showing suppres-
sion could have either strong or weak visual
interaction effects. Even a short series of
experiments (24 cells, 10 showing suppres-
sion) showed that suppression does not
necessarily compensate for a weak visual
interaction effect.

Nor was the visual interaction between
stimuli limited to any sublayer of the super-
icial layers. We were unable to observe any
relationship between the strength of the
visual interaction effect and the depth in
the penetration where a cell was encountered.
We confirmed this impression from single-
cell recording by making several penetrations
with larger electrode tips in order to record
multiple-cell activity; we found a forward
visual interaction effect as long as we had
visual responses. Thus the visual effect ex-
tends throughout the superficial layers, as
does the suppression effect (R. H. Wurtz,
B. J. Richmond, and M. Mishkin, un-
published observations).

Discussion

We have found three types of visual inter-
actions in the cells of the superficial layers
of the monkey superior colliculus: interac-
tions generated by a stimulus as it crosses,
successively, the surround and then the
center of the receptive field; interactions
between two successively presented stimuli
falling within the central area; interactions
between two successively presented stimuli,
one of which is remote from the conven-
tionally defined receptive field. During sac-
cadic eye movements, each of these visual
interactions probably contributes to a reduc-
tion in the response of colliculus cells to
the visual stimulation resulting from the eye
movements. We would like first to discuss
these interaction effects individually, and
then relate them to the previously observed
trends in visual sensitivity due to remote
stimulus effects and to corollary discharge.

Visual interactions relevant to saccades

The first type of visual interaction results
from the receptive-field properties of the
visually responsive cells in the monkey
superior colliculus. Several investigators (2,
4, 16) have found that in the center of these
receptive fields, which we refer to as a cen-
tral activating area, a spot of light pro-
duces an on- and usually an off-response,
while the surrounding or flanking area, which
we refer to as the suppressive surround,
yields no on- or off-responses to stimuli, but
instead reduces the response to concurrent stimuli falling in the central area. While there seems to be little spatial summation within the central area of the field (smaller stimuli are more effective than larger ones), summation is the rule in the surround since larger stimuli are more effective (4). The suppressive effects of the surround area undoubtedly extend into the central area since larger stimuli wholly within the central area frequently give a less vigorous response than do small stimuli (4, 16).

We found that when a moving stimulus sweeps over both the central area and the surround area of the receptive field, the response is frequently very slight, if present at all, but that the response can be greatly strengthened by allowing the rapidly moving stimulus to cross only a small region in the center of the excitatory receptive field. Under this condition all of the collicular cells responded to rapid stimulus movement, and we were able to duplicate the response to rapid stimulus movement by briefly flashing a stimulus in the same central region of the receptive field crossed by the moving stimulus. This is consistent with the earlier observations of Robinson and Wurtz (15) that cells with weak surrounds tended to respond more frequently to rapidly moving stimuli than did fields with powerful surrounds. The visual interaction effect must be an important influence on visual processing during saccades made under natural conditions because stimuli would probably cross both the activating center of the receptive field and the suppressive surround. One might almost view this effect as a self-mask ing of receptive-field surround on receptive-field center.

A consequence of this center-surround interaction for the response of collicular cells to moving stimuli is that the superior colliculus should be most sensitive to rapid movements of discrete stimuli when the stimulus remains within the central area of the receptive field. Hence, the optimal size movement should be smaller near the center of gaze than in the periphery because the central area of the visual receptive fields is generally smaller near the center of gaze than in the periphery (2, 4, 16). The difference in response to rapid stimulus movement is what Robinson and Wurtz (15) found; using an arbitrary length stimulus movement (20°), cells with receptive fields within 5° of the fovea responded less frequently to moving stimuli than did cells with receptive fields 10–20° from the fovea.

The second type of visual interaction effect, the reduction of response to a brief stimulus falling in the receptive-field center when a prolonged stimulus preceded it, is as prominent in the superior colliculus as it is in striate cortex (8). The time course and strength of the forward visual interaction effect are about the same as that seen in cells of striate cortex (8). Cells in the superior colliculus would also be subject to the "confounding" of the response to the sweep or flash stimuli with the response to a subsequent prolonged stimulus. The relevance and limitations of the visual interaction effects on the response of cells during saccades is comparable to that discussed for the striate cortex (8).

The larger size of the receptive-field centers in the colliculus compared to those in striate cortex offered the opportunity to see if the visual interaction between stimuli continued to occur when the two stimuli were spatially separated. We found that a prolonged stimulus that fell on a part of the visual receptive field different from that of a subsequent brief stimulus continued to reduce the response to the brief stimulus. A noise pattern was also an effective, but less powerful, prolonged stimulus. Thus, for eye movements, a stimulus pattern falling on any part of the central receptive-field area before a saccade should decrease the response of the cell during an eye movement even if different parts of the central area are stimulated during the eye movement. Such an arrangement obviously maximizes the potential for visual interaction between presaccadic and saccadic stimuli.

The similarity of the strength and time course of the visual interaction effect between stimuli in superior colliculus and striate cortex reinforces the possibility that the visual interaction effect between successive stimuli could logically occur in the retina and then be transmitted to both cortex and colliculus. While the subsequent experiments showing that visual interaction within the center of the receptive field occurs with substantial separation between
stimuli are more easily understood as interactions within large collicular receptive fields, remote effects in the retina (1, 3, 9, 10) cannot be ruled out. The most conservative hypothesis now is that the interaction develops at each successive station in the visual pathway.

The third type of visual interaction occurs when a stationary stimulus placed well outside the receptive-field center is turned on before a stimulus is flashed within the center. Like the effect of the conventional surround, the effect is also a suppressive one; the remote stimulus neither increases nor decreases the discharge rate of the cell when presented alone, it only reduces the response to a stimulus falling in the central area of the receptive field. The remote stimulus is effective when it is in the same visual hemisphere as the receptive field, but much less so when it is across the vertical meridian in the opposite hemisphere. We would expect this type of remote visual interaction to be important during eye movements since contours in the visual scene need not even fall onto the conventional receptive-field area to be effective, but the possibility has not been tested during saccadic eye movements.

The interaction of one stimulus on another when the first is placed well outside the center of the visual receptive field, the periphery or shift effect, has been reported in the retina of the cat and monkey (1, 3, 9, 10). The effect is seen primarily in Y-type cells (for example, Refs. 1, 9), which provide a large proportion of afferent activity from the retina to the superficial layers of the superior colliculus (6, 17). However, the periphery effect in the retina usually produces an increase in responsiveness in the center of the receptive field rather than a decrease, as in the colliculus, and the periphery effect does not decrease as the remote stimulus crosses the vertical meridian, as it does in the colliculus. These differences suggest that the mechanisms that mediate the periphery effect are not likely to be the same as those that mediate the remote interaction effect in the colliculus.

Remote interaction and attention

The effect of a remote stimulus on the response to a stimulus within the central area of the receptive field is similar to an effect originally reported on cells in the superior colliculus of the cat by Rizzolatti et al. (13, 14). They found that moving a stimulus remote from the central area of the receptive field attenuated the response to a stimulus moving within the center. Our observations in the monkey are similar to those in the cat in that both suppression effects occur with small stimuli remote from the center of the central activating region of the receptive field, both show a reduction in suppression when the remote stimulus is in the contralateral hemisphere, and both show a reduction in suppression when the interval between the presentation of the remote stimulus and the stimulus in the receptive-field center is increased. But there are also differences in experimental tests and results: as the distance between the remote stimulus and the stimulus in the central area of the receptive field increases, the suppression effect decreases in the monkey, but stays more nearly constant in the cat (14); the remote stimulus need not move in the monkey, whereas the remote stimulus was always moved in the cat (14).

Rizzolatti et al. (14) speculated that the remote inhibition effect might be a correlate of attention, but insofar as we are observing a similar phenomenon in monkey and cat, we think we can reject the attention hypothesis. While in the paralyzed cat it is difficult to know what stimuli are able to attract attention, in the awake monkey we have an excellent estimate of this. In our task the monkey must respond to a fixation light but need not respond either to the receptive-field stimulus or the remote stimulus. The latter two stimuli are not behaviorally relevant and the monkey does not shift his gaze to them. The remote effect depends on the stimulus conditions, not on the monkey's response to the stimuli. On the other hand, the visual enhancement seen in many of these superficial layer cells does depend on the monkey's behavior and occurs only with stimuli that become the target of saccadic eye movements (5, 19). The enhancement effect is found in only approximately one-half of the superficial superior colliculus neurons, while the remote interaction effect is present in the great majority of cells tested. Thus, the remote interaction effect appears to be a purely visual one that is
distinct from the visual enhancement or suppression effects seen to accompany saccades.

Visual interaction and corollary discharge

Cells in the superficial layers of the superior colliculus not only show visual interaction effects that would reduce their response to visual stimulation during saccadic eye movements, but they frequently also show suppression of background rate and reduction in visual sensitivity following each eye movement (4, 12, 15). It is not immediately obvious why two such overlapping mechanisms exist.

The visual interaction effect depends on the presence of a contoured stimulus on the visual receptive field of a cell before a saccade. If a saccade were made across a bright stimulus, starting from a relatively low contrast scene, the colliculus cells (as well as striate cortex cells) would respond to the bright stimulus. In the case of perception, such a stimulus is seen as a sweeping blur under these circumstances: a distant street light in the dark, indicator lights on equipment in an otherwise darkened room. Insofar as the superior colliculus is related to monitoring the visual surround for behaviorally important stimuli so that the eye can be directed to such stimuli, it might be essential that stimulation that is self-induced by a rapid eye movement be eliminated under all conditions, including those of low contrast. We have been impressed with how readily cells in the superficial layers of the superior colliculus respond to stimuli even a few tenths of a log unit above the ambient illumination, and these cells would obviously be very sensitive under conditions of low luminance and contrast. But the suppression of discharge rate and the related reduction of sensitivity of the colliculus cells function under all conditions, high and low luminance, large or small contrast. The corollary discharge to the colliculus might be protecting the saccadic system from false triggering under most natural stimulus conditions.

The opposite question then comes to mind: if a powerful suppression mechanism is so useful in the superior colliculus, why not have it available to the striate cortex as well? One answer to this question is the need to detect stimuli during saccades, as discussed in the preceding paper (12). Another answer to the question may be related to the suppression of background activity that accompanies the reduction in visual sensitivity seen in the superior colliculus. In the striate cortex, it is impressive how little the rate of discharge of cells is modified by saccades. No pause occurs at the time of the saccade; the discharge rate just changes from that related to the stimulus falling on the receptive field of the cell before the saccade to that of the stimuli falling on the receptive field after the saccade. This cellular activity is a reasonable facsimile of the perceptual changes accompanying saccades: there is no pause or grayout, but simply a shift from one visual scene to another. If there were as clear an extravisual input to the striate cortex as there is in the superior colliculus, then there would be a suppression of the background activity with each saccade. Such a suppression might then be evident perceptually as a pause in continuous vision, which of course we do not experience. The stimulus interaction effects we have seen obviate this problem for the neurons in striate cortex and might well do so for perception as well.

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