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# Activity of Superior Colliculus in Behaving Monkey. III. Cells Discharging Before Eye Movements

ROBERT H. WURTZ AND MICHAEL E. GOLDBERG

*Laboratory of Neurobiology, National Institute of Mental Health, Bethesda, Maryland 20014*

CLINICAL CORRELATIONS (13) and stimulation studies beginning in the last century (1, 4, 12, 22, 28) have provided the evidence for the view that the superior colliculus is involved in the neural generation of eye movements. Physiological studies have concentrated on sensory input to the colliculus, and it has been established that cells in the superficial gray and optic layers of the rhesus monkey superior colliculus have well-defined visual receptive fields (10, 15, 24). The response of roughly half of these cells is markedly enhanced by the monkey's intention to use the stimulus falling in the receptive field of the cell as the target of a saccade, but this enhancement depends on the visual stimulus; in the absence of visual stimuli these cells lose their striking activity before eye movements (11). On the other hand, cells in the intermediate gray and white layers of the colliculus do discharge before saccadic eye movements of specific distance and direction, even in total darkness (24, 30). This report describes the properties of these cells.

A brief report (30) and an abstract (8) of some of these results have been presented previously.

## METHODS

The general behavioral and physiological methods used were the same as described in the two preceding papers in this series (10, 11).

Cells in these experiments were studied under two conditions. First, whether or not the cell had a visual receptive field was determined while the monkey fixated a small spot of light (as in the first paper of this series, ref 10). Second, the monkey was induced to make a saccade or tracking eye movement. A saccade was produced when the fixation point went off and a second point came on and became the fixation point (11). A tracking eye movement was produced by moving the fixation point in a smooth arc as long as 20°. This was done at speeds ranging from 5 to 125°/sec by reflecting the fixation point off a front-silvered mirror and by applying a ramp waveform to the galvanometer on which the mirror was mounted.

Lateral rectus electromyograms were made using chronically implanted ball electrodes placed on Tenon's capsule through a hole drilled in the squamous portion of the parietal bone. The presence of the small EMG electrode had no measurable effect on the velocity or frequency of eye movements.

Points in a microelectrode penetration where interesting cells were recorded were marked by an electrolytic lesion and located on histological sections.

## RESULTS

In eight monkeys, 70 cells were recorded that gave a burst of cell discharge preceding saccadic eye movements. Electrolytic lesions made through the recording electrode at the site of these cells were located primarily in the intermediate gray and white layers of the superior colliculus with a few points in the deep gray layer. Figure 1 shows one of these lesions that was located at the edge of the intermediate gray layer.

### *Cell activity and eye movement*

The superior colliculus neurons described in this study all increased their rate of discharge before eye movements of specific direction and distance. The time of onset of the burst varied from cell to cell. Some neurons clearly increased their rate of discharge as long as 200–300 msec before the EOG deflection, others only 30–50 msec before the EOG deflection. Since the cell

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discharges associated with eye movement frequently had a slow and irregular onset (as in Fig. 2) and developed against an irregular background, these times of onset can only be regarded as rough estimates. The patterns of discharges of four different cells which started to discharge at different times before the deflection of the EOG associated with the eye movement are shown in Fig. 2. In *A* the cell shows a burst of discharges within 30 msec of the start of the EOG. In *B* and *C* the increased rate of discharge begins at least 100 msec and 150 msec, respectively, before the eye movement. In *D* discharge rate increases 300 msec before the eye movement although a burst occurs within the 50–100 msec just before the eye movement. Figure 2 also shows that cells frequently continued to discharge at a higher rate during and somewhat after the eye movement. Others stopped discharging with the eye movement.

While these neurons all began to discharge before the eye movement occurred as measured by the EOG, we also wanted to make certain that the bursts of discharges preceded activity in the eye muscles. We therefore recorded lateral rectus electromyograms simultaneously with the EOG and unit responses in two monkeys. In Fig. 3 the EMG burst preceded the EOG by 15 msec, and in general the EMG preceded the

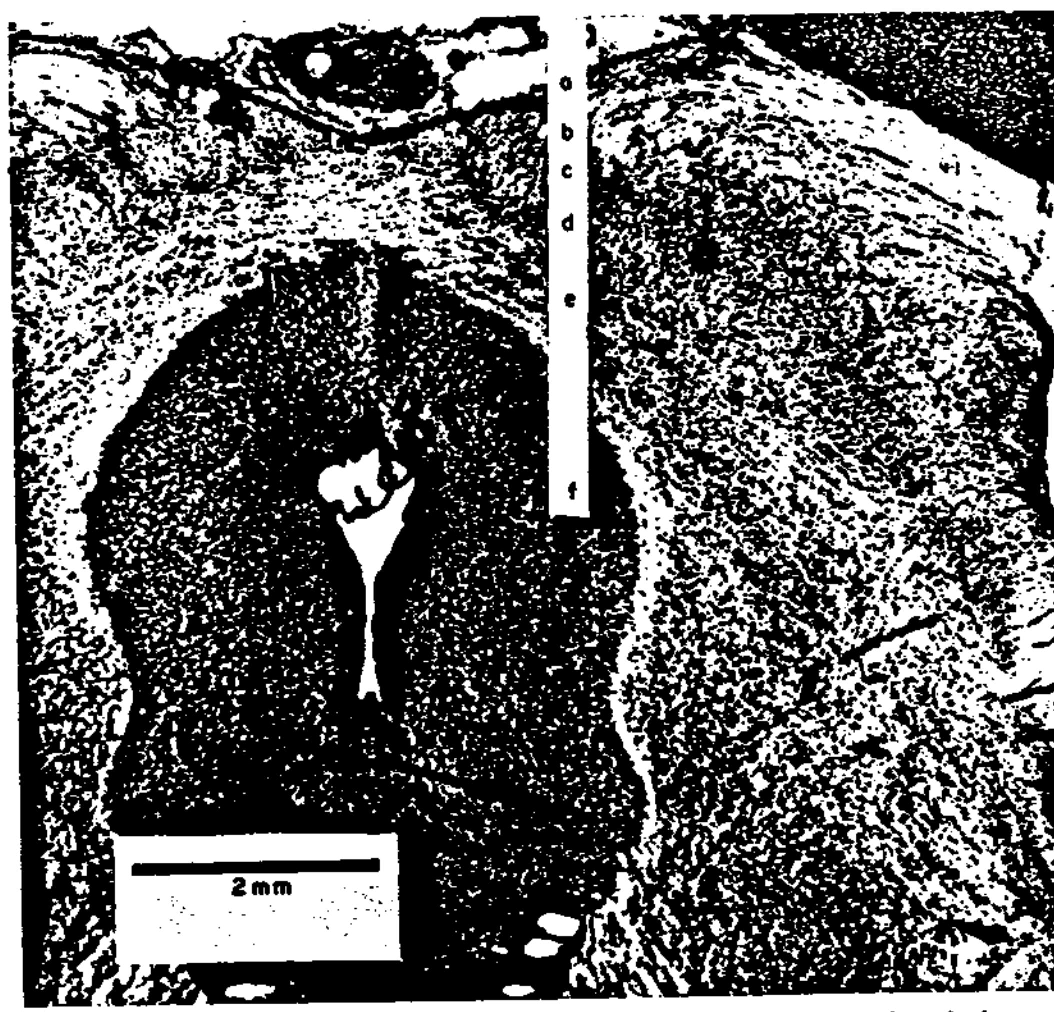


FIG. 1. Location of movement-related cells in the superior colliculus. Cresyl violet-stained coronal section with lesion produced through the microelectrode at edge of intermediate gray layer. a, superficial gray layer; b, optic layer; c, intermediate gray layer; d, intermediate white layer; e, deep gray and white layers; f, central gray.

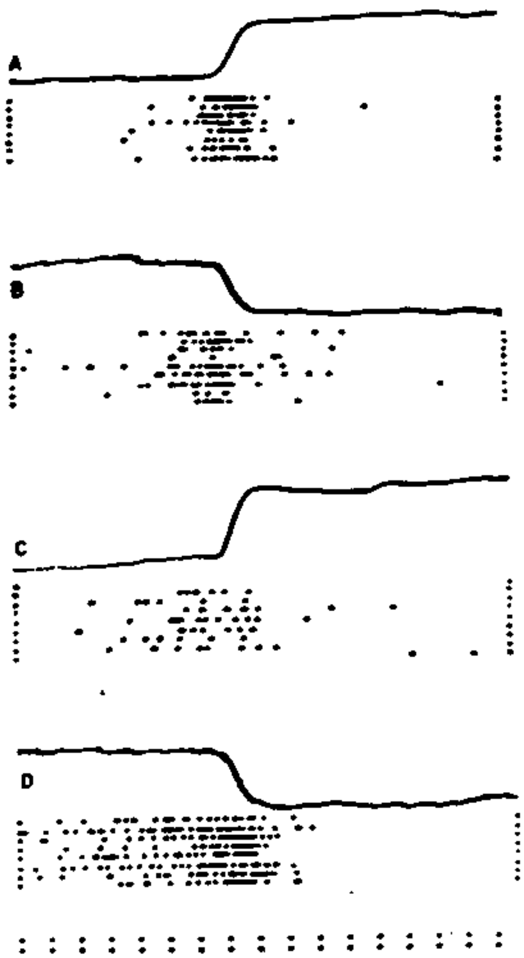


FIG. 2. Relationship between cell discharges and eye movement. In each section a dot represents the discharge of the cell and the beginning and end of each line; successive lines show discharges associated with successive eye movements. The four cells in sections *A–D* discharge at progressively earlier times before the eye movement and show varying patterns of discharge during and after the eye movement. In each section the lines are synchronized with the eye movement and a sample of the eye movement used is shown above each section. An indication of the regularity of these trained eye movements is given in the records in the next paper (31). Time interval between successive dots on time line is 50 msec in this and all subsequent dot pattern figures.


FIG. 3. Relationship of EMG, EOG, and cell discharges. Middle trace is EMG of right lateral rectus; lower trace is horizontal EOG associated with a 20° horizontal saccade from left to right.

These cells also discharged before saccades regardless of what elicited the saccade. The eye movements routinely studied were saccades made from one spot of light to another, and Fig. 4*A* shows a cell discharge before such a saccade. Each cell also discharged before spontaneous eye movements made in light or dark and Fig. 4*B* shows the same cell as in Fig. 4*A* discharging before a similar eye movement made spontaneously in total darkness. The time between the onset of cell discharges and the eye movement was approximately the same

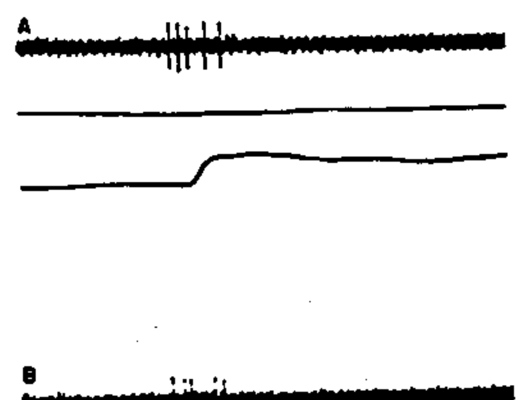


FIG. 4. Cell discharges preceding eye movements made in the light (*A*) and total darkness (*B*). Middle trace is horizontal EOG, bottom trace is vertical EOG. In *A* the eye movement was made to a point 20° up from the fixation point; in *B* a spontaneous eye movement was selected so that the vertical and horizontal EOG closely resembled the EOG associated with the controlled eye movement in *A*. This cell had no visual receptive field.

EOG by 10–20 msec. Since the superior colliculus neurons related to eye movement all started to discharge at least 30–50 msec before the eye movement, they preceded activation of the eye muscles by at least 10 msec. Therefore, the burst of cell discharges did not result from sensory feedback from extraocular muscles.

for the visually guided movement (Fig. 4*A*) and the spontaneous movement in the dark (Fig. 4*B*). This burst of cell discharges related to eye movement can therefore occur in the absence of any retinal stimulation.

Whether or not the cell discharged during vestibular nystagmus was tested by irrigating one ear with cold water while the monkey was in total darkness. Those cells that discharged before a horizontal saccade comparable in length to the eye movements in nystagmus also discharged before the fast phase of horizontal nystagmus. The discharge of these cells is therefore related to vestibularly elicited eye movements as well as to those visually elicited or occurring spontaneously in total darkness.

*Movement fields*

The discharge pattern of a particular cell was related only to eye movements made to a given area of the visual field. We determined this area by having the monkey make a saccade repeatedly from a fixation point on the tangent screen directly in front of him to some other point on the tangent screen. By producing saccades to different areas in the visual field, we were able to find a set of target points associated with presaccade cell discharges. The target points always lay within one area of the visual field, and we will refer to this area as the movement field of the cell in analogy to the receptive field of a visual neuron. Figure 5 shows the outline of a movement field. Plusses indicate points where saccades were associated with cell discharges, zeros where saccades were not. The right side of Fig. 5 shows the gradation of cell discharges for eye movements to points on the line through the movement field. Just inside the field (with a 20° eye movement) the burst was slight while farther into the field (with 35–40° eye movements) the burst was more vigorous. The burst was slight along the entire medial edge of the movement field (along the solid line) and more vigorous in the center and lateral edge of the field.

The movement field of every cell studied was located predominantly in the visual field contralateral to the side of the superior colliculus where the cell was located. In Fig. 5 the movement field slightly overlapped the vertical meridian. For other cells with movement fields centered closer to the vertical meridian, the cell frequently

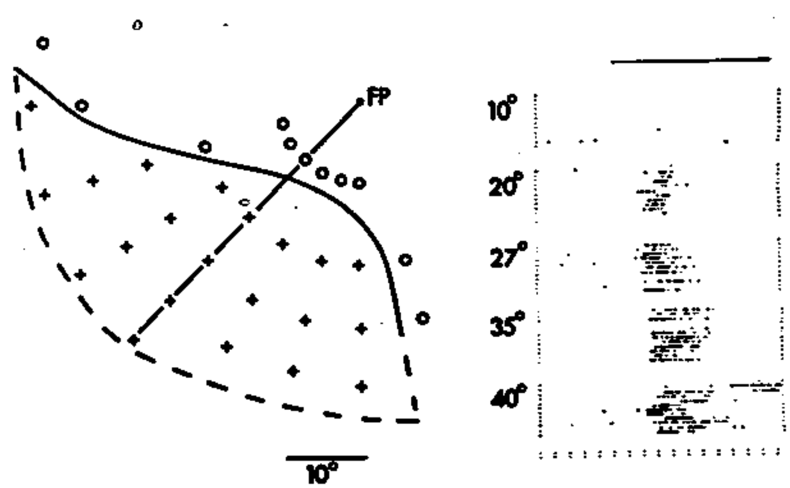


FIG. 5. Movement field of superior colliculus neuron. Each point on the drawing indicates the correlation of cell discharges to an eye movement made from a point straight ahead of the monkey (fixation point, FP) to the points shown. *A*: + indicates the correlation of cell discharges with the eye movement; O indicates no correlation. The curved solid line shows the medial border of the movement field; the dashed line indicates the lateral border of the area tested since eye movements longer than 40° were usually made by the monkey as two saccades in tandem rather than as one saccade. The cell discharge patterns at five sample points along the straight line in the movement field are shown in the dot patterns on the right; eye movements were 10–40° long. In this figure and in Figs. 8 and 9 a correction has been made in plotting the amplitude of large eye movements to allow for the error introduced by the use of a tangent screen.

discharged before eye movements to the ipsilateral visual field but the maximal discharge rate always occurred with eye movements directed vertically or to the contralateral visual field.

*Movement fields and visual receptive fields*

The feature that these neurons in the intermediate layers had in common is that they increased their discharge rate before an eye movement to an appropriate area of the visual field. About 60% of these cells also responded to visual stimulation. In Fig. 6*A*, for example, the cell responded when a spot of light came on in its receptive field even though no movement occurred. In Fig. 6*B*, the same cell responded with a short latency to the spot of light but then continued to discharge as the monkey made an eye movement to the spot of light. Thus a visually elicited eye movement was preceded by a roughly biphasic pattern: first a response to the onset of the stimulus with a latency of about 40–50 msec, and then a burst of discharges before the eye movement that followed the stimulus by roughly 150 msec but preceded the eye movement by at least 100 msec. Figure 6*C* shows the same responses as in Fig. 6*B* but with the display triggered on the eye movement rather than the stimulus; the later discharges are well synchronized with the eye movement, the early discharges are not.

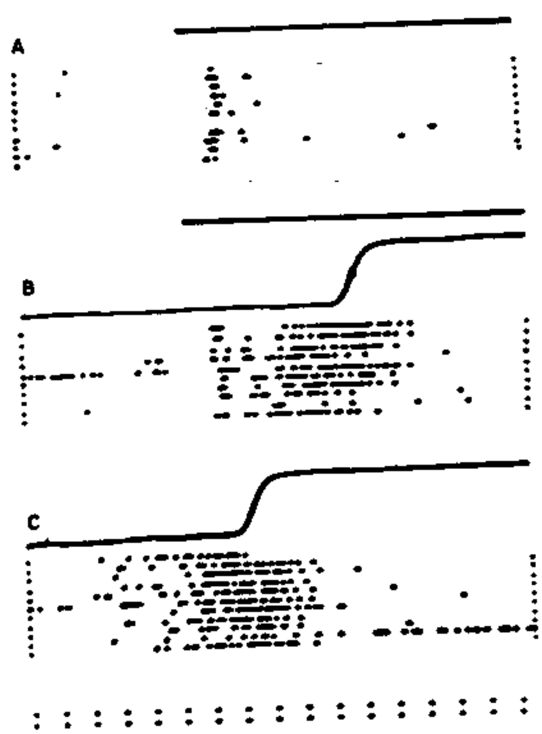


FIG. 6. Response of a cell following onset of a spot of light and preceding the eye movement to the spot. *A* shows the cell discharges with successive presentations of a 1° spot of light (onset shown by solid line) in the receptive field of the cell. *B* shows the discharges of the cell following onset of the spot of light (indicated by solid line) but preceding the eye movement (indicated by one sample horizontal EOG) to the spot of light. In *C* the same discharges shown in *B* are again shown but are synchronized with the eye movement rather than the stimulus as in *B*.

The visual receptive fields and the movement fields of these cells always lay in the same general area of the visual field but were generally not coterminous as shown in Figs. 7 and 8. In Fig. 7 the area of the movement field (outlined by the solid line) was larger than the area of the receptive field (dashed line), but the receptive field lay in that part of the movement field with the most vigorous activity before eye movements (Fig. 7, left side). This congruence of maximal movement-associated activity with maximal visual response was observed in all cells. Both the movement field and the visual field showed gradients in discharge frequency from the more central areas of the field to the edge of the field; the visual field just covered a smaller area. In Fig. 8 the visual receptive field (outlined by a dotted line medially and a dashed line laterally) was larger than the movement field (solid line medially, dashed line laterally). In the dot pattern on the left the cell discharges associated with both the onset of the spot of light and a saccade to the spot (*A* column) are compared to the response to the onset of the spot with no saccade (*B* column). Again, the maximal cell response preceding eye movement was in the same area (*A*, 3, 4, 5) as the best response to the onset of the spot of light (*B*, 3, 4, 5).

In studying these cells we used the technique utilized in the preceding paper to study the enhancement of a visual response: the spot of light falling in the receptive field was used as the target of a saccade (11). We generally did not see an enhancement of the on-response in movement-related cells (as in Figs. 6 and 7) and when the enhancement was present it was very slight (Fig. 8, points 8 and 9).

Cell types were encountered in an orderly sequence in a penetration through the intermediate gray and white layers of the colliculus. Cells with both receptive fields and movement fields were encountered just below the cells in the optic layer. Then as the penetration extended deeper into the intermediate layers, cells with only movement fields and no receptive fields predominated.

Since the visual receptive fields in the rhesus monkey superior colliculus are topographically organized (10), and since the movement fields are in the same area as the receptive field, it follows that there is a similar topographic organization of the movement fields in the intermediate layers of the colliculus. This topographic relationship holds both for cells with visual and movement fields and for those with only movement fields.

*Slow pursuit eye movements*

There was no indication that these movement-related cells increased their rate of discharge during slow pursuit eye movements. For example, in Fig. 9 the cell did not discharge regularly with pursuit movements made to a spot moving at 5 or 10°/sec. When the spot moved at speeds between 20 and 125°/sec, the unit did discharge but these bursts always preceded a corrective saccade made to catch up with the moving spot, and were probably not related to the smooth pursuit components of the eye movements. Other cells in the intermediate layers did discharge during slow pursuit movements, but they appeared to be related to the visual stimulus guiding the pursuit

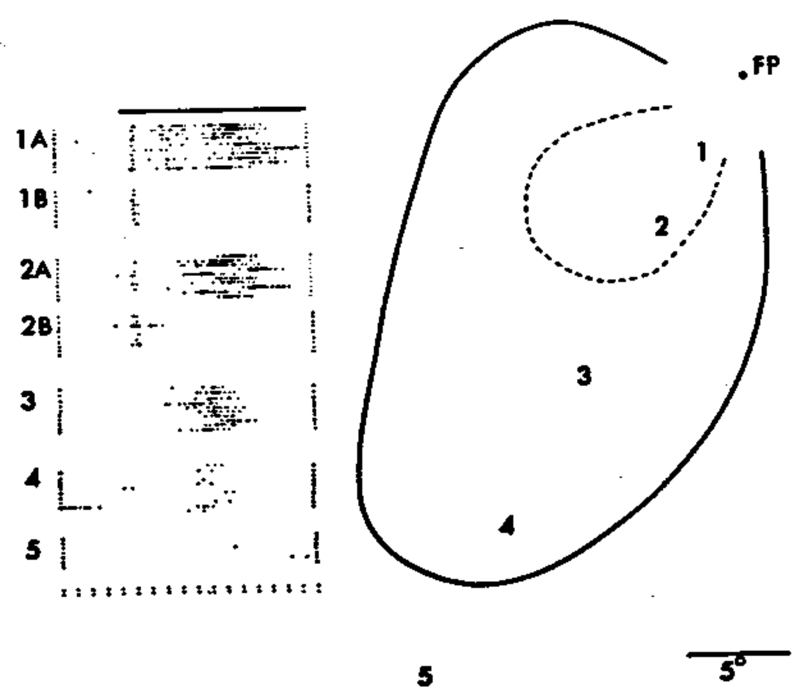


FIG. 7. Cell with a visual receptive field smaller than its movement field. In the drawing the dashed outline of the receptive field was determined by finding the cell's response to stationary spots of light at various points in the visual field (ref 10, Fig. 2). The solid line outline of the movement field was obtained as in Fig. 4 of this paper. The open medial edge of the field was not determined since it was difficult to be certain the monkey did or did not make small eye movements to this area. The response of the cell preceding the eye movement at points 1–5 is shown in the dot patterns on the left. For points 1 and 2, which are in both the visual receptive field and the movement field, the cell discharge is shown when an eye movement was being made to the spot of light (1A, 2A) and when only the spot of light came on with no eye movement being made (1B, 2B).

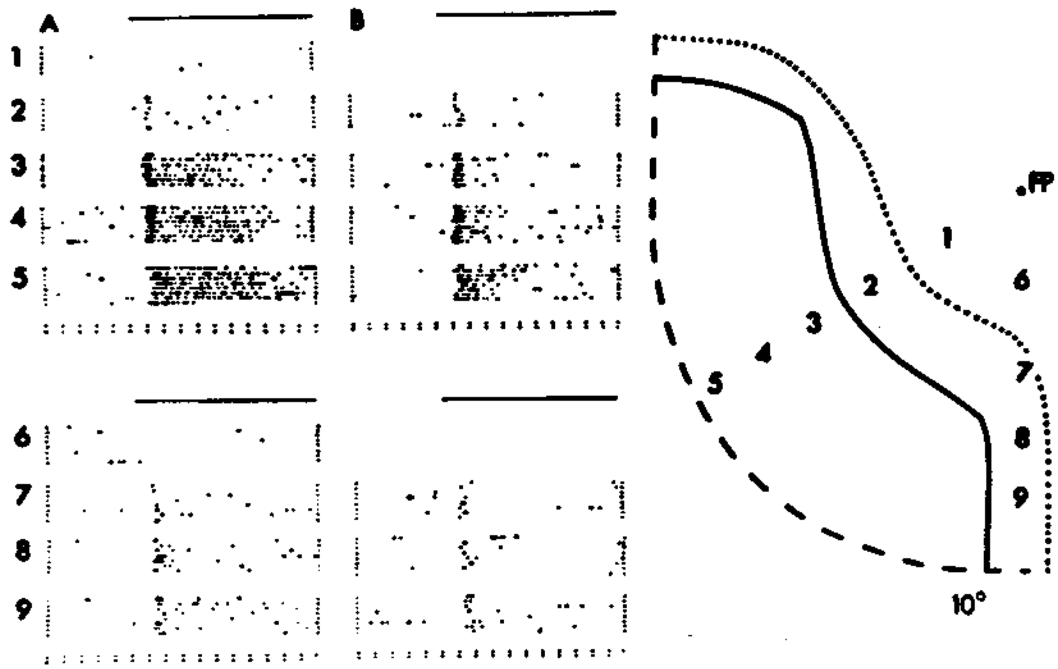


FIG. 8. Cell with a visual receptive field larger than its movement field. The dotted line outlines the medial edge of the visual receptive field and the solid line outlines the medial edge of the movement field. The lateral edge of both fields is indicated by a dashed line since it could not be determined exactly because of the limited saccade length obtainable. The cell responses obtained at a series of points are shown in the dot patterns on the left; in column *A* the monkey made a saccade to the spot of light which came on at the time of the indicator line, while in *B* the monkey made no saccade when the spot came on. Points 1–5 are in a line through both the visual receptive field and the movement field; points 6–9 are in a line through the visual receptive field only.

movement rather than the pursuit movement itself (9), and they will not be considered further here.

### *Direction and position of movement*

Most of these neurons related to movement discharged before a movement of a given length and given direction, regardless of where the starting point of the movement was. For example, in Fig. 10 a 10° long downward-directed saccade was made in each of the four quadrants of the visual field. The bursts of cell discharges before the movements were very similar and these bursts were therefore related to the eye movement independent of the position of the eye.

We have, however, encountered some cells with discharge patterns related to eye position. Figure 11 shows a cell which discharged tonically when the monkey fixated various points in the upper left quadrant (Fig. 11*A*), but not when he fixated various points in the lower right quadrant (Fig. 11*B*). Other cells discharged in relation to both eye movement and eye position or stopped discharging during eye movement. These cells tended to have no visual receptive fields and to be located deep in the colliculus bordering on the deep gray layer. Both the discharges related to eye position and the pause in discharge with eye movement are similar to discharge patterns found recently in pontine reticular formation neurons (25; and E. S. Luschei and A. F. Fuchs, personal communication). We have not studied these cells deeper in the colliculus in detail.

## DISCUSSION

### *Characteristics of movement-related cells*

Neurons related to eye movement in the intermediate gray and white layers of the monkey superior colliculus discharge only before eye movements to a particular area

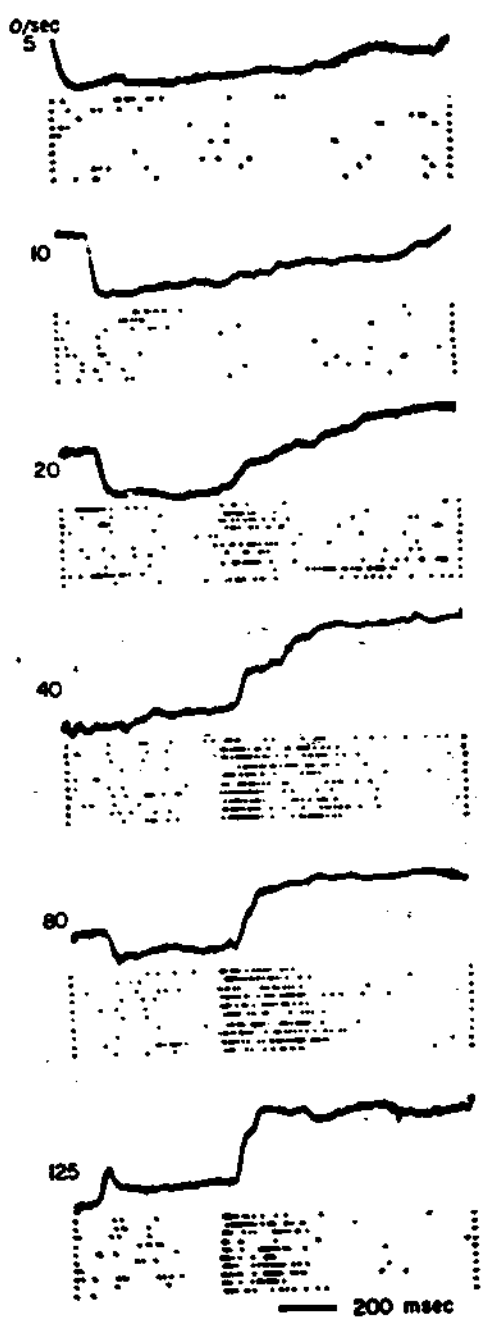


FIG. 9. Slow-pursuit eye movements and cell discharge. Speed of target movement and one sample horizontal EOG for the horizontal 20° long eye movements are shown for each section. Cell discharge became clear when corrective saccades became clear at a 40°/sec track speed.

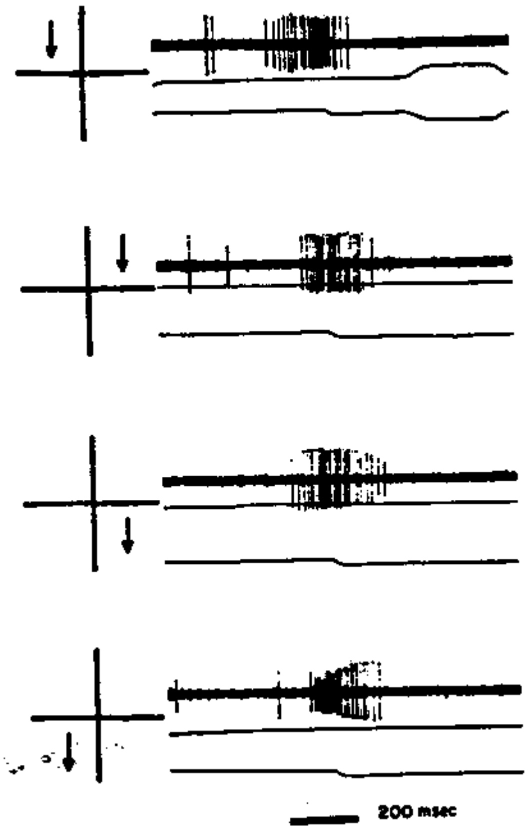


FIG. 10. Cell discharge related to eye movement not eye position. Discharge of the cell is shown preceding the same size eye movement made in each of the four quadrants of the visual field. In the drawing the center of the cross indicates the point on the tangent screen directly in front of the monkey. Arrows represent a 10° downward saccade made starting at a point 20° over and 20° up (or down) from the center of the field. The middle trace is horizontal EOG, the bottom trace is vertical EOG.

of the visual field; we call this area the movement field of the neuron, a term analogous to the receptive field of a sensory neuron. The movement fields of collicular neurons lie primarily in the contralateral visual field. They tend to lie in the same area of the visual field as do the retinotopically organized visual receptive fields of the neurons just above them in the superficial gray and optic layers of the colliculus (10).

Since the movement field is retinotopically organized, it moves in space as the eyes move, and a saccade of proper distance and direction is preceded by a burst of discharges regardless of the initial position of the eye. In keeping with this, these cells do not seem to have any component of their discharge pattern related to eye position

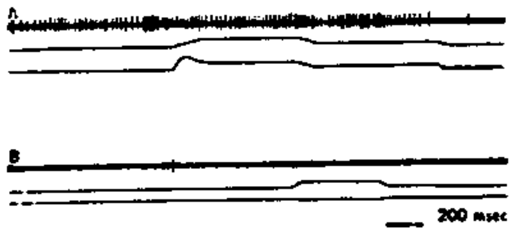


FIG. 11. Cell discharge related to eye position. In *A* the monkey is fixating points in the upper left quadrant of the visual field. Note that the discharge rate varies with eye position. In *B* the monkey is fixating various points in the lower right quadrant, none of which are associated with cell discharge. The middle trace is horizontal EOG, bottom trace is vertical EOG. The d-c level of the EOG was balanced between *A* and *B*.

(except for a few cells deep in the colliculus which we have not studied in detail). This similarity between the maps of visual receptive fields and eye movement fields corroborates the original work of Apter (3, 4) in the cat and Robinson (22) in the monkey who found that the map of final position of eye movements evoked by stimulating the superior colliculus closely corresponded to the map of the retinal projections. Robinson's stimulation experiments also showed that repeated stimulations caused repeated saccades, with the termination of each saccade serving as the initial point for the next, and this is further evidence that in the monkey superior colliculus eye movements are organized according to the retinal position of their targets, rather than according to which muscles will be necessary to effect the movement.

Some of the cells are not only movement related, but also have visual receptive fields. The visual receptive fields lie in the same area of the visual field as the movement fields, but the boundaries of the visual receptive field and the movement fields are rarely coterminous; sometimes the visual field is bigger, sometimes the movement field. These cells have two types of discharge patterns: a burst associated with the onset of a stimulus in the receptive field and a lower frequency more tonic increase in discharge rate before an eye movement. The burst occurs whether or not the stimulus becomes the target of a saccade; the premovement activity occurs whether or not a stimulus evoked the eye movement.

The sufficient event for a burst of discharge of any of these neurons is a rapid eye movement to the movement field of the neuron; the movement-related burst is independent of the stimulus evoking the eye movement. Indeed, the cells respond similarly before visually guided saccades, spontaneous saccades in total darkness, and the fast phase of caloric nystagmus. This invariance serves to differentiate this class of neurons in the intermediate layers from a class found in the superficial layers that seem also to be related to eye movement. The necessary stimulus feature for one of these superficial cells is a spot of light in its receptive field. If the monkey intends to generate a saccade to the stimulus, the cell has an enhanced response to the stimulus which may continue up to the eye movement; this enhanced response resembles the movement-related response of the cells in the intermediate layers, but it disappeared in total darkness. Of the 78 cells related to eye movement and visual stimulation recently described by Schiller and Koerner (24), 70 did not respond in total darkness and most of those cells must therefore have been the type of cell considered in the preceding paper (11), rather than the neurons described in this study which discharge before the eye movement regardless of the stimulus. Straschill and Hoffman (27) did find cells in the superior colliculus of the encéphale isolé cat with activity related independently to eye movement alone and visual stimulus alone.

Since we studied these neurons in animals with rigidly held heads, we cannot say whether or not these cells are also related to neck movement. Bizzi, Kalil, and Tagliasco (5) showed that in the rhesus monkey eye and head movements are intricately linked, and suggested that neck and eye muscle EMG patterns might remain unchanged even when the head is immobilized. The activity of superior colliculus neurons might also, therefore, be related to head and neck movement as well as eye movement.

*Function of movement-related cells*

In this study we have seen a continuation of a series of cell types in the monkey superior colliculus that seems to progress from analysis of a stimulus to preparation for a response. Cells in the superficial layers respond to light. Cells in the bottom of the intermediate layers respond only before eye movements. In between these two there are two stages of transition: the cell type that responds to light but that has an enhanced response when the animal is going to fixate the light (11), and the cell type that discharges independently either to a visual stimulus or before an eye movement. It is tempting to postulate that the cells with only the movement-related activity are close to the output of the superior colliculus and that this activity has been constructed as a result of the visual and behavioral input to the more superficial cells. However, we have neither anatomic nor physiological evidence for such functional connections, nor need the connections be direct from one cell type to the next.

Cells discharging before a movement can have several functions. One function could be as a corollary discharge, feeding information from the motor system back to the sensory system. Since Helmholtz, it has been thought that information about the motor commands positioning the eyes (referred to as corollary discharge or efference copy) might be integrated by the brain along with the information from the retina in order to construct a stable visual world (14, 26, 29). Johnstone and Mark (17, 18) described neurons in the fish tectal commissure that discharged before eye movements in specific directions. Since the fish appeared to have normal eye movements after sections of the commissure or ablation of the tectum, Johnstone and Mark postulated that the neurons were not involved in the generation of eye movements but instead performed an efference copy role. By these criteria, the cells we describe in the monkey superior colliculus could be called efference copy neurons since monkeys with collicular lesions can move their eyes (2, 20, 31). However, we feel that in the monkey superior colliculus the evidence is not strong enough to assign such a function to these neurons. First, we do not know how these neurons, or the ones in the upper layers which are inhibited during eye movements (10), modify their response to visual stimuli at the time of an eye movement as one would expect if they had a corollary discharge function. Second, we would expect ablation of a significant corollary discharge system to produce a deficit in behavior rather than no deficit. While no gross loss of eye movements occurs after ablation of the monkey superior colliculus (2, 20), a closer analysis of eye movements does reveal a deficit, which we shall consider in the next paper (31), but one not obviously related to a corollary discharge deficit. Because of this lack of evidence, we are reluctant to ascribe a corollary discharge function to neurons in the superior colliculus, but we also do not want to exclude the possibility.

A second function of the movement-related cells could be to act as part of the neural mechanism controlling eye movements. If these superior collicular neurons are upper motor neurons for eye movements, they must be several synapses away from the lower motor neurons for several reasons. First, the discharge of these neurons on a retinotopic map must be somehow translated into the orbital position map used by the lower motor neurons; second, we find that collicular cells start to discharge as early as 200–250 msec before eye movements as compared to 2–12 msec for oculomotor neurons (7, 21, 23); third, the monkey superior colliculus is not known to send fibers to any of the oculomotor muscle nuclei although it does have a projection to the pontine reticular formation (19) which may be involved in the generation of eye movements (25).

In ascribing any motor function to these cells one must deal with the problems posed by their large receptive fields and movement fields. The fields are more than an order of magnitude larger than the accuracy of a monkey's saccade. For example, in a 20° saccade a monkey overshoots the target by only 0.5° (6), but the collicular movement fields 20° from the fixation point are usually at least 10–20° in diameter. One of these neurons by itself cannot specify the parameters of a saccade or specify the position to which the eye is going to move. They can, however, indicate a rough area of the visual field and facilitate movement to this area.

We tested this view of the function of the superior colliculus by studying the effect of lesions in the superior colliculus on the eye movements of monkeys as described in the following paper (31).

SUMMARY

Neurons in the intermediate gray and white layers of the monkey superior colliculus discharged before rapid eye movements of specific distance and direction. The discharge pattern was the same before equivalent eye movements regardless of the stimuli used to evoke the eye movement; visually guided saccades, spontaneous saccades in total darkness, and the fast phase of caloric nystagmus were all preceded by cell discharges.

The necessary eye movements were best described as movements to fixate a certain area of the visual field. This area of the visual field, defined as the movement field of the neuron, was situated in the contralateral visual field, and was retinotopically organized in the same way as the receptive fields of adjacent visual neurons in the more superficial layers of the superior colliculus. The discharge pattern of the movement-related neurons was independent of the initial position of the eye in the orbit.

Some neurons had visual receptive fields as well as movement fields. The visual receptive fields of these neurons were in the same area of the visual field as their movement fields, but were not necessarily coterminous. The visual response could be dissociated from the movement-related discharges by presenting the monkey with a visual stimulus in the absence of eye movements, or by looking at the relationship of the cell discharges to eye movements in the dark.

These movement-related neurons by themselves cannot specify the parameters of a saccade or specify the position to which the eye is going to move. We suggest instead that these cells specify only a rough area of the visual field and facilitate movement to this area.

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