The role of the monkey superior colliculus in eye movement and vision

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Our work during the past few years has concerned itself with the function of the mammalian superior colliculus. Working jointly with M. Stryker and F. Körner, we studied the effects of superior colliculus ablation on orientation and pattern perception in the monkey. We recorded single units in this structure and we studied the effect of stimulation in cats and monkeys, using both the alert and anesthetized preparations. I am happy to say that much of our work is in close agreement with that of the previous speaker, Bob Wurtz.

For this presentation, I will focus on our recording and stimulation work.

Single unit recordings in the superior colliculus

One of the striking things we find when looking into the literature is that the functional organization of the superior colliculus is markedly varied in different mammalian species. Thus, in the ground squirrel, as reported by Michael, many units seem to be specific to stimulus orientation and direction of movement, suggesting that in this animal the colliculus might play a role in pattern perception. In the cat, as shown by many investigators, there is very little evidence for specificity in terms of stimulus orientation, but a great deal of directional selectivity; thus, about 70 per cent of the units appear to respond preferentially to stimulus movement in certain directions. Nearly all of the units in the colliculus have binocular input. The optimal stimulus is often smaller than the receptive field; the surround is antagonistic.

Large stimuli or diffuse light typically fail to drive these units.

In the monkey we find one major difference in the functional characteristics of collicular units. In this animal we do not observe any directional selectivity. The size of the fields is also quite a bit smaller than in the cat. In the superficial layers the best response can be obtained to smoothly moving stimuli. When one advances the electrode further into the colliculus of the monkey, a subtle change can generally be observed. About 0.9 to 1.5 mm. down, cells no longer respond to smooth movement. Instead, the optimal stimulus becomes one which is displaced in the receptive field in a jerky fashion or which is flashed on. The responses are brief, with a short burst of spikes to both onset and offset of the stimulus.

Two of my graduate students, Max Cynader and Nancy Berman, who compared the cat and monkey, also found some interesting differences in the topography of the superior colliculus. Fig. 1 shows this. In the monkey we have a larger representation of the macular area. Most interesting perhaps, is the finding that in the monkey there is no ipsilateral representation which is so evident in the cat. I should add here that in the Siamese cat this ipsilateral representation is about twice as extensive as that in the domestic cat.

What I have discussed so far is based mostly on recordings in the anesthetized, flaxedilized animal. Before proceeding further, I would like to briefly mention the effects of visual cortex ablation under such recording conditions. Although some controversy exists, the weight of the evidence

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suggests that ablation of the visual cortex in the cat generally produces two dramatic effects while leaving other receptive-field characteristics unchanged. Binocularity and directional selectivity are reduced under such conditions, suggesting that these attributes may be mediated by cortex.15

We have done similar work in the monkey, much of it still is in progress. So far we find that in the superficial layers one observes very little change after removal of visual cortex. Binocularity is not affected and receptive-field characteristics remain unchanged.

Next, I would like to turn to our findings in the alert monkey. We were interested in studying both receptive-field characteristics and eye movement, and so we developed the preparation in which one eye is immobilized by transection of the third, fourth, and sixth cranial nerves, and eye movement electrodes are implanted around the moving eye.19 During recording sessions the head is restrained6 and microelectrodes are lowered into the colliculus via an implanted well.

This preparation allows us to map receptive fields via the immobilized eye and to study eye movements via the moving eye.

The characteristics of superior colliculus cells in the superficial layers of this preparation are very similar to those I already described; thus, anesthesia does not seem to produce any dramatic changes in this respect. In the lower layers, however, we found characteristics which would not be found in the acute preparation. In these layers eye movement cells predominate. A typical example of such a unit is shown in Fig. 2.

The unit, as can be seen, fires prior to certain saccades, which in this case are small and in the left-up direction. Other saccades, either in different directions or in the same direction but of a larger magnitude, are not associated with unit activity.

This unit also has a visual receptive field, as shown in the bottom tracings. A flashing stimulus activates the cell, although not nearly as vigorously as the eye movement. This was generally the case for such
Fig. 2. Discharge characteristics of a unit related to eye movement. A, B, and C, Unit discharge and eye movement in the light, moving eye unoccluded. D, Response to a 0.25 degree light spot moved back and forth within the receptive field of the immobilized eye with a square wave; moving eye occluded.
units. Visual stimuli in themselves were not very effective. About 80 per cent of eye movement–related units we studied had this dual property. The remainder responded only in association with saccades, and were typically found deeper down in the colliculus.

We were interested in determining the specificity of these units. Do they fire to saccades of specific sizes and directions or do they fire when the eye comes to a certain place in orbit? Our analysis suggests the former. If one looks at discharge activity in terms of saccade size and direction irrespective of eye position prior to the saccade, one comes up with a map like the one shown in Fig. 3. Circles represent saccades not associated with unit activity; discs show those saccades which were preceded by a burst of spikes. As can be seen, this unit fired in association with small left and up saccades. The size of these motor fields varied greatly among the units studied. Some were smaller than this one, and others much larger, even as big as 20 to 30 degrees. The visual receptive fields of these units were typically in that region of the visual field relative to the fovea to which the eye moved as a result of the saccade-associated burst. In other words, if one were to transform this motor map here into a visual map, the receptive field of the unit would lie in the same area in which unit discharge–associated saccades are located.

**Stimulation studies**

Stimulation of the superior colliculus has been shown to elicit eye movements, although there is some disagreement as to what the nature of such eye movements might be. In the alert rabbit one apparently obtains smooth-pursuit eye movement upon stimulation of the superior colliculus. Similar slow movements can also be obtained under some conditions in anesthetized cats and monkeys. In alert cats and monkeys, however, one typically obtains saccadic eye movements. Let me first describe what was found in alert
monkeys by David Robinson and also by us, and then I'll return to the cat to highlight some issues.

We have stimulated in the alert monkey using the preparation I just described. We first record single units and then stimulate through the same microelectrode.

To clarify the eye movement response, I thought it might be informative to compare the effects of stimulating the lower layers of the superior colliculus with stimulation of the abducens nucleus. This is shown in Fig. 4.

When one stimulates in the abducens at a fixed frequency, 500 Hz. in this case, a saccade is obtained which varies in size, as might be expected, with the duration of the burst. A similar change in saccade size can also be obtained when one keeps the duration constant and varies frequency. Frequency variation also affects the velocity of the saccade; higher frequencies produce faster eye movements.

The story in the superior colliculus is very different. Here, within the ranges shown, the size of the saccade is influenced neither by frequency nor by duration of electrical stimulation. Interestingly, if the duration is made long enough, one obtains additional saccades with intervening fixations. The size and direction of the saccades depends on the site of stimulation. On the bottom of the figure is shown a long series of saccades which was obtained by stimulating the anterior region of the colliculus. Looking at the monkey one might have thought this was smooth pursuit. But we have never really succeeded in getting reliable smooth pursuit with collicular stimulation, and neither has David Robinson.

In the monkey the size and direction of stimulation-elicited saccades is independent of the location of the eye in orbit. Thus, the same saccade is obtained when the animal prior to the saccade looks to the left, right, up, or down.

Returning to the technique of stimulating through the same microelectrode from which we are recording, our aim of course was to look for the relationship between unit activity and stimulation. We thus compared the activity of eye movement-related units in the manner I described earlier and the effects of stimulation at the same site. A map of this sort is shown in Fig. 5. Discs represent saccades associated with unit activity; X represents stimulation-elicited saccades. I think it is evident that the two maps are similar. For the 25 cells
we have studied so far, the saccade sizes and directions with which the unit fired was the same as that obtained to stimulation. Generally we found that the stimulation produces greater specificity; in this map too, the motor field to stimulation is smaller. I should also note here, that one needs very little current in this region to elicit a saccade. One to 9 µAmps are sufficient. This current, which is actually less than required in the abducens to elicit a saccade, is so small that we do not destroy the units; thus, we can record from the same unit after stimulation.

In the superficial layers one needs considerably more current to elicit eye movement, usually from 400 to 1000 µAmps. In these layers, Mike Stryker and I compared saccade sizes and directions elicited by stimulation with the distances and directions of the receptive field from the fovea. A double map of this sort is shown in Fig. 6.

How do these data compare with those from the cat? In the cat, eye movement-related cells have also been reported, although not analyzed in the same manner. The most provocative stimulation study in this animal is still that of Julia Apter, who put strychnine crystals on the colliculus and found that subsequent diffuse light stimulation produced eye movements. The impression gained was that the eye moved to a certain location in orbit. Often neglected is Apter’s observation that repeated flashes of diffuse light moved the eye still further in the orbit, although with much smaller saccades. Unfortunately, most descriptions deal with 16 to 20 degree initial saccades which in the cat bring the eye close to the limits of ocular mobility.

Straschill and Rieger did experiments in the cat very similar to ours; they stimulated through the same microelectrode from which they recorded single units. They report that the eye goes to a certain place in the orbit independent of initial eye posi-
The example I saw was also for rather large eye movements.

We are presently repeating some of this work in the cat. Our impression so far is that the cat is like the monkey, but not quite as neat. An example is shown in Fig. 7. You can see that repeated stimulation moves the eye over in steps; long bursts produce staircases. But it is also evident that the first saccade is larger than subsequent ones. This becomes more pronounced as one moves posteriorly in the colliculus; initial saccades get larger, and drive the eye close to its limits and so subsequent ones are smaller or practically nonexistent. Finally, we also know that if the cat is free, prolonged stimulation produces saccades followed by head turning, and if the stimulation is long enough, body turning as well. In fact, one can make a cat rotate all the way around.

These observations then, taken together, suggest that some sort of eye-centering mechanism may be operative in the colliculus. This is seen as an eye movement to acquire a target; subsequent orientation in terms of head and body movements reflect further ramifications of this activity. In exactly what sense the colliculus contributes to this is still open to debate; it is unclear whether we are dealing with attentional, sensory, and motor channels or in some combination of all of these. It is unlikely, however, in view of the evidence presented, that the coding is still in terms of an eye-orbit relationship.

Interpretation is also rendered difficult by the fact that the colliculus is indeed not
Fig. 7. Saccades elicited by electrical stimulation of the cat superior colliculus. Top tracings show spontaneous eye movements. Middle tracings show saccades elicited upon successive 300 Hz., 70 msec. duration stimulus bursts. Bottom tracings show staircase with prolonged stimulation.

the only structure which produces the kinds of conjugate eye movements I described. Matter of fact, such eye movement responses are rather ubiquitous. Thus, we know from Robinson and Fuch's work that stimulation of the frontal eye fields of the alert monkey produces similar effects to those I described for the colliculus. The same applies to visual cortex. This is shown in Fig. 8. Three maps are shown, one for the frontal eye fields, one for the superior colliculus, and one for visual cortex. Here again, the point is that saccade size and direction are independent of the initial eye position in orbit. Staircases are also obtained in these two cortical areas, and the duration-frequency independence persists. However, the current levels required are strikingly different. In the lower layers of the colliculus, as I noted, 1 to 9 μAmps will do it. In the frontal eye fields one may need 30 to 500 μAmps. In visual cortex the range is 200 to 2,000 μAmps. Finally, we have some evidence that ablation of the superior colliculus eliminates the eye movements elicited via visual cortex stimulation but preserves the effects of frontal eye field stimulation.

These findings suggest that saccadic eye movement activity may be mediated through several channels, and that the role of visual cortex in this function may be mediated through the superior colliculus.

REFERENCES
Fig. 8. Stimulation-elicited saccades in the frontal eye field (FEF), superior colliculus (SC), and visual cortex (VC) of the alert monkey. A single site was stimulated in each of the three structures. Dot represents fixation point in the visual field prior to stimulation. Line and arrow show size and direction of the saccade produced by the stimulation.


Discussion

Pettigrew: Could the effects you get from stimulating the contralateral abducens simply be a release from inhibition?

Schiller: You refer to my statement that in our preparation stimulation of the contralateral abducens, where the sixth nerve has been cut, one can elicit ipsiversive saccades of the normal eye. One cannot rule out the possibility of a simple release from inhibition. However, it seems to me that if this were the case, we would get only slow, drifty eye movements rather than the crisp saccades we observed. Therefore, I rather prefer the idea that excitation is propagated through existing channels to the third nucleus, activating that part of the nucleus which innervates the medial rectus of the moving eye. This could be brought about either by stimulation of cells within the abducens or of the fibers in the immediate vicinity of the nucleus.

Wurtz: I want to comment that the movements we see are just as you are describing, i.e., retinotopic. The thing we have not seen are units which you are describing as “jerk detectors.” Do you think that the microsaccades in our monkey eyes are the reason for the difference?

Schiller: It hadn’t occurred to me, although it is a possibility. I can only say that we are confident of the transition I described; the visual units which we begin to see about 0.9 mm. below the surface of the colliculus respond very poorly or not at all to smooth stimulus displacement. Berman and Cynader in my laboratory have also observed this, although to a lesser extent, in acute preparations where the animal is flaxedilized and anesthetized with N2O.

McLWAIN: Buser and I noticed a lot of units in the cat which you might characterize as “jerk detectors,” i.e., exquisitely sensitive to small movements. Historically, Apter’s pioneering experiment is certainly compatible with a retinotopic map also since her stimuli were given when the eye was in a position of rest.

Hubel: When you stimulate the cortex the saccades you got were about 20 degrees or so? Were you in a corresponding part of the cortex?

Schiller: You are referring to the last figure. Let me answer you by saying that in visual cortex the relationship between receptive-field location and the elicited saccades is much worse than in the superior colliculus. This is probably due to the fact that in visual cortex one needs
anywhere from 200 to 2,000 µAmps to elicit eye movement. This means considerable current spread, so that we could be stimulating the fibers of the underlying white matter, some of which may be quite remote in terms of retinal topography.

DAW: Did you look for visual receptive fields in the frontal eye fields?

SCHILLER: Yes we have, but only in one animal so far, in which we studied about 50 units. We did not find any visual receptive fields for these cells.

ROBINSON: The lack of smooth pursuit movements with punctate stimulation doesn’t mean that they are not in a structure there. The use of more refined electrical stimuli might bring them out.

SCHILLER: You are quite right. Matter of fact, on the basis of our single unit work we gained the impression that the eye movement cells in the anterior tip of the colliculus discharged not only in association with small saccades but also in association with certain pursuit movements. So we fully expected that when stimulating in this region with continuously varied frequencies we might get pursuit. This seemed to work sometimes in the dark, but I am not really convinced. It is clear, however, that in the light we never succeeded in eliciting smooth pursuit eye movement.

Some effects of visual deprivation on the cat superior colliculus

Barbara Wickelgren-Gordon

Recently a great deal of interest has arisen in the physiologic and behavioral effects of depriving young animals of normal visual input. I have been interested in the effects of visual deprivation on the superior colliculus, not primarily as a developmental problem, but in order to compare the effects of deprivation on the colliculus with its effects on the lateral geniculate nucleus and visual cortex. I hoped that this comparison would provide some additional insight into the different roles that the cortex and colliculus play in the processing of visual information and into the elaboration of collicular receptive fields from their retinal and cortical inputs. Before describing some new data on the effects of artificial squint on the colliculus, I would like to review some of the work that has contributed to current notions about the function of the colliculus and about the elaboration of collicular receptive fields.

Functions of the colliculus

The classical concept of the mammalian visual system includes the notion that the superior colliculus controls visual orienting and following responses while the geniculostraliate system subserves detailed pattern perception. This notion has received support and refinement from a number of recent experiments. Cells in the cat colliculus are much less sensitive to receptive field size, shape, and orientation than are cortical cells. On the other hand, collicular cells are extremely sensitive to stimulus movement, responding optimally only to moving stimuli. Collicular cells are usually directionally selective; however, they respond well over a much wider range of directions than do directionally selective cortical cells. Collicular cells are primarily sensitive to the direction of the horizontal component of stimulus movement, usually

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