The primate superior colliculus and the shift of visual attention

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The primate oculomotor system can generate eye movements in response to visual stimuli. The superior colliculus, long thought to be a component of that system, occupies a transitional point in the oculomotor system. It receives input directly from the retina and indirectly from the visual cortex,[9, 22] and many investigators have demonstrated cells with visual receptive fields in the superior colliculus of monkeys and other mammals.[17] In the primate, the anatomic connections to the motor nuclei of the extraocular muscles are not direct.[11] However, stimulating the colliculus results in eye movements[14] and single cells in the colliculus discharge before voluntary eye movements.[15, 20, 23]

Although it is clear that the superior colliculus is in the pathway between the visual stimulus and the eye movement, the role played by the colliculus in the process of generating a visually guided eye movement is not at all clear. One view of colliculus function is that it provides the target information necessary for the accurate guidance of eye movements.[13-15] However, two different lines of evidence are highly dissonant with this view. The first is that monkeys without superior colliculi show no gross deficit in visually guided eye movements.[1, 12] The second is that the functional properties of the cells in the monkey superior colliculus, which have large receptive fields or respond before eye movements to very large areas of the visual fields, do not appear to be appropriate for the exact guidance of eye movements.[4, 24] Another view of the colliculus is that it mediates the shift of visual attention which must precede the actual displacement of the eye during a visually guided eye movement. In support of this view we will discuss several aspects of our experiments on the superior colliculus in awake monkeys. This work has been published in detail,[4, 5, 24, 25] and in this brief report we will present only those results necessary for an understanding of our arguments.

Methods

Monkeys were trained to fixate a spot of light on a tangent screen in front of them.[4] The monkey pressed a bar to turn on a spot of light on the screen. One to three seconds later, the spot dimmed and remained dim for half a second. If the monkey released the bar while the light was dim, he received a reward. Otherwise he received neither reward nor punishment. The monkey was sufficiently interested in the fixation spot that he would not break fixation to look at another light which was flashed on the screen. This second light could be used to determine the receptive field of the cell under study. The methods of Evarts[2] were used to hold the head rigidly and to

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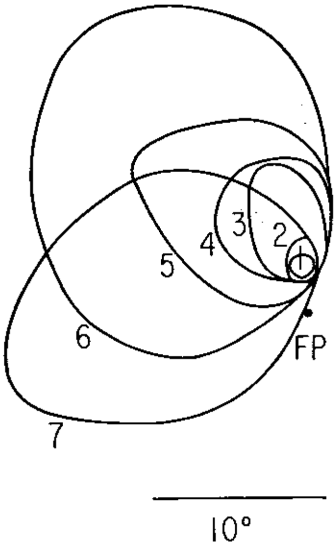

Fig. 1. Increase in receptive field size with increasing depth in superficial layers of superior colliculus. The seven receptive fields were for cells encountered in the order in which they are numbered. *FP* indicates position of fixation point. Fields were mapped using 0.2 to 0.5 degree stationary spots of light. (From Goldberg and Wurtz: J. Neurophysiol. **35:** June-July, 1972.[4])

record the activity of single cells in the superior colliculus while the monkeys were performing their tasks. Eye movements were measured with direct current (DC) electrooculograms (EOG). Electrolytic marking lesions were made through the electrode at the sites of interesting cells, and the brain was examined histologically to ascertain the location of the lesions.

Intracollicular construction of large receptive fields

Receptive fields were found for all cells studied in the superficial gray and optic layers of the superior colliculus. The great majority (almost 90 per cent) of the cells responded to stationary spots of light and to spots of light moving in any direction through the receptive field. The cells were remarkably insensitive to many stimulus parameters. The cells responded to all stimulus orientations as well as directions of motion. Spots a fraction of a degree in diameter had the same effect on the cells as spots that included the entire excitatory area; the only limiting factor was an inhibitory surround, which restricted the size of effective stimuli for about 80 per cent of the cells. The receptive-field size of the cells was large relative to that of cortical and retinal ganglion cells[6, 8] and, for a given penetration in the colliculus, increased in size with depth of the cell in the first two layers. Fig. 1 shows the receptive fields of seven cells obtained in a penetration nearly perpendicular to the surface of the superior colliculus. The excitatory area of each field is outlined and nearly contains within it the area of the receptive field just above it. Receptive fields also became larger as the location of the field was further from the fixation point, and, as reported previously,[17] the visual field is mapped retinotopically on the contralateral colliculus. This organization is in striking contrast to the organization of the visual cortex, wherein hierarchies of cells extract finer and more sophisticated aspects of stimulus parameters. The colliculus, on the other hand, seems to us to degrade much of this information, sacrificing stimulus detail in order to be able to say only within a very large field where a stimulus lies.

Modification of stimulus effect by attention

Half of these cells had the striking property of responding not only to the physical parameters of the stimulus but also to the behavioral parameter of how the monkey was going to respond to it. The receptive-field characteristics of the cells considered so far were all determined while the monkey looked at the fixation point. There was no indication that the monkey paid any attention to the spots of light falling on the receptive field of the cell; he had seen the spots of light thousands of times previously and was not rewarded for any change in the receptive-field stimulus. We next determined what change in the response of the cell occurred when the monkey was forced to pay attention to the spot of light falling on the receptive field of the cell being studied by requiring the monkey to use the receptive-field stimulus as the target for a saccade. The experiment was done as follows: First, while the monkey looked at the fixation point, the response of the cell to a spot of light falling on the previously determined excitatory central area of the receptive field was determined for ten to 20 trials. Then the experimental conditions were changed so that at the same time that the receptive-field stimulus came on, the fixation point went off. In previous training, the monkey had learned that under this condition he must saccade to the receptive-field stimulus since that spot might now dim and release of the bar during that dim would be rewarded. The monkey indicated that he had shifted his attention to the receptive field stimulus by making a saccade to the stimulus, which was recorded on the EOG. However, there was a reaction time to make the saccade of about 200 to 300 msec., and it is during this time that the critical results of the experiments were obtained. During this time the eye had not moved so the receptive-field stimulus was the same as on previous nonsaccade trials. But the significance of the stimulus had changed; it had now become the target of the saccade.

The results of using this method of directing the monkey's attention to the receptive-field stimulus are shown in Fig. 2. In *A*, the monkey was looking at the fixation point, and on successive trials the receptive-field stimulus came on at the indicator line. In *B*, as the receptive-field stimulus came on the fixation point went off, and the monkey saccaded to the receptive-field stimulus; the saccades occurred near the end of the line. The response of the cell to the visual stimulus was more vigorous on most trials and more regular on successive trials during this period when the monkey was paying attention to the stimulus than when he was not. In *C*, the conditions were returned to those in *A;* the monkey no longer saccaded to the receptive-field stimulus and the response returned to the original level within a number of trials. The enhancement was not only a more vigorous ON response as in Fig. 2, but was also frequently a prolonged discharge beyond the initial ON response. Other cells showed a combination of the early ON response enhancement and addition of the later response (for example, Fig. 3).

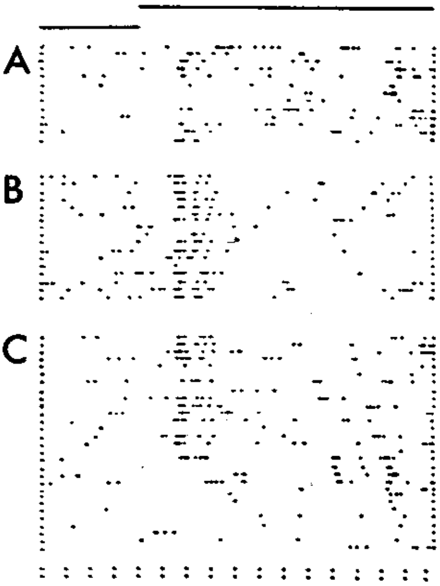

Fig. 2. Enhancement of the ON response of a cell to the receptive-field stimulus. Each cell discharge and the beginning and end of each line is indicated by a dot. Successive lines of dots represent successive fixations. The line above the figure indicates approximately when the receptive-field stimulus came on. In *A* there was no saccade to the receptive-field stimulus, in *B* the monkey saccaded to the receptive-field stimulus, and in *C* he did not saccade to it. The time between dots on the bottom two lines is 50 msec. in this and subsequent figures. (From Goldberg and Wurtz: J. Neurophysiol. 35: June-July, 1972.[5])

A critical point in the analysis of this enhanced response is whether it was selectively related to certain stimuli which were the target of the eye movements (and thus could be reasonably regarded as related to attention) or whether it was related to any eye movement to any part of the visual field (and therefore might be related to a more general activation or arousal level). To test the selectively of the enhanced response, we allowed the monkey to saccade to either of two spots of light as shown schematically in the top of Fig. 3. Each time the fixation point went off, two other spots of light came on, the receptive-field stimu-

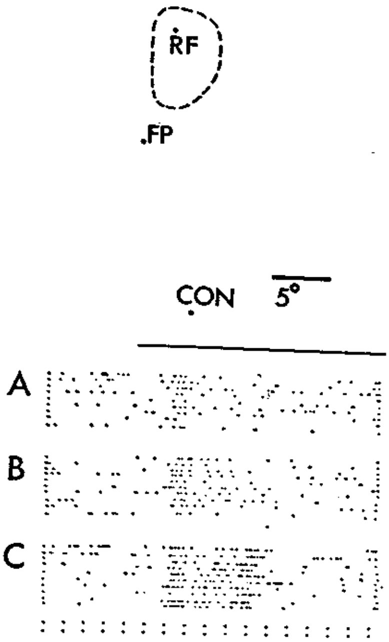

Fig. 3. Selective effect of response enhancement. In *A*, no saccades were made away from the fixation point, in *B* the monkey saccaded to the control stimulus with little response enhancement, in *C* to the receptive-field stimulus with clear response enhancement. Cell was one that habituated rapidly. See text for details of the experiment. (From Goldberg and Wurtz: J. Neurophysiol. **35:** June-July, 1972.[5])

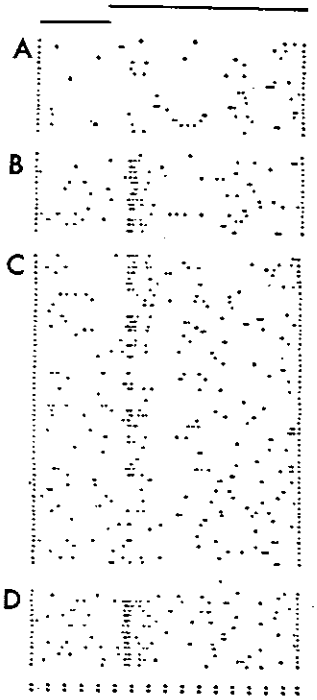

Fig. 4. Habituation of ON response. In *A* the monkey was not saccading to the receptive-field stimulus while in *B* and *D* he was. In *C* the monkey was not saccading to the receptive-field stimulus at all but the enhanced response persisted over a number of trials. (From Goldberg and Wurtz: J. Neurophysiol. **35:** June-July, 1972.[5])

lus (labeled *RF*) and a control stimulus (labeled *CON*) outside the previously determined receptive field of the cell. The monkey could and did saccade to either of these stimuli since the reward was equally related to eye movements made to either one of the stimuli. Fig. 3, *A*, shows the responses of the cell to the receptive-field stimulus coming on when no saccade was made to any stimulus. In *B*, those trials when the monkey saccaded to the control stimulus (as determined from the EOG records) are shown; there was slight, if any, enhancement. In *C*, those trials in which the monkey saccaded to the receptive-field stimulus are shown; the enhancement of the ON response and presence of a late response are clear. The enhancement effect, therefore, is selective; the cell's response to a stimulus was enhanced only when the monkey was using stimuli in the area of the receptive field as the target of the saccade. This selective attention effect is superimposed on a more general level of alertness presumably necessary to perform the fixation task.

While the monkey attended to the receptive-field stimulus by saccading to it, the response of the cell to the stimulus did not habituate with successive stimulus presentations. However, as soon as the fixation point stopped going off as the receptive stimulus came on, the monkey stopped saccading to the receptive-field stimulus, since there was no longer any reason for doing so. But even though the saccading had ceased, the discharge of the cells frequently did not return to the previous level immediately but showed a gradual habituation, brief as in Fig. 2, or more prolonged

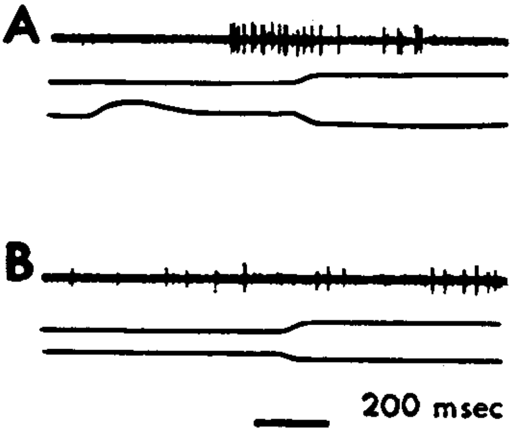

Fig. 5. Comparison of cell responses in light and dark. The cell is in superficial layers and responds before eye movement to the stimulus (*A*), and the response is enhanced over the no-saccade condition) but not before a similar eye movement made in total darkness (*B*). Upper EOG trace is horizontal, lower vertical. (From Goldberg and Wurtz: J. Neurophysiol. 35: June-July, 1972.[5])

as in Fig. 4. Thus when the monkey was attending to the receptive-field stimulus, habituation began and the response of the cell to the stimulus was reduced to its previous level. This strongly suggests that lack of attention leads to habituation of the response of collicular cells to light stimulus. The previous reports of habituation in the colliculus of paralyzed animals[7, 10, 18, 21] may also relate to a change in attention to the stimulus which could not be measured or controlled. Whether habituation of single cell responses in other parts of the visual system and in other sensory systems is reciprocally related to attention must be determined by further experiments.

While these experiments have used an eye movement to indicate that the monkey was attending to a stimulus, we do not believe that the associated enhancement effect was simply a result of the eye movements since the enhancement was not tied to eye movements in any one-to-one manner. As just noted, the enhancement effect frequently continued during a habituation period after the eye movements to the stimulus had ceased. In addition, these cells never responded before a spontaneous eye movement to the large receptive-field areas when such eye movements were made in total darkness. In Fig. 5 for example, the cell responded before an eye movement to the stimulus (*top trace*) but not before an eye movement to the same area made in total darkness (*bottom trace*). The presence of a stimulus was a necessary condition for observing the attention effect; eye movement was the way in which attention was objectively identified but was not a necessary condition for the enhancement effect.

Relation of intermediate layer cells to eye movement

Unlike the cells in the upper layers of the colliculus, cells in the intermediate gray and white layers discharged before eye movements to a particular area of the visual field. They discharged before the proper eye movements regardless of the conditions under which the eye movement was made: saccades to a visual target, random saccades in total darkness, or even the fast phase of vestibular nystagmus. The eye movement–related activity of these cells was independent of orbital position and depended only upon the position of the saccade target being in one area of the visual field. We call this area of the visual field the *movement field* of a cell, in analogy to the visual receptive field of a sensory cell, and, indeed, the movement field of an intermediate layer neuron lies in the same area of the visual field as the receptive fields of the cells in the superficial layers just above them. Fig. 6 shows the outline of a movement field of a collicular cell. The dot patterns on the left show the discharge associated with eye movements and emphasize the gradation of cell discharge toward the edge of the movement field (similar to the gradation of response for visual receptive fields in the upper layers). Fig. 6 also shows (*dashed lines*) that the cell had a visual receptive field which was mapped while the monkey fixated. This combined movement and receptive field was common for cells first en-

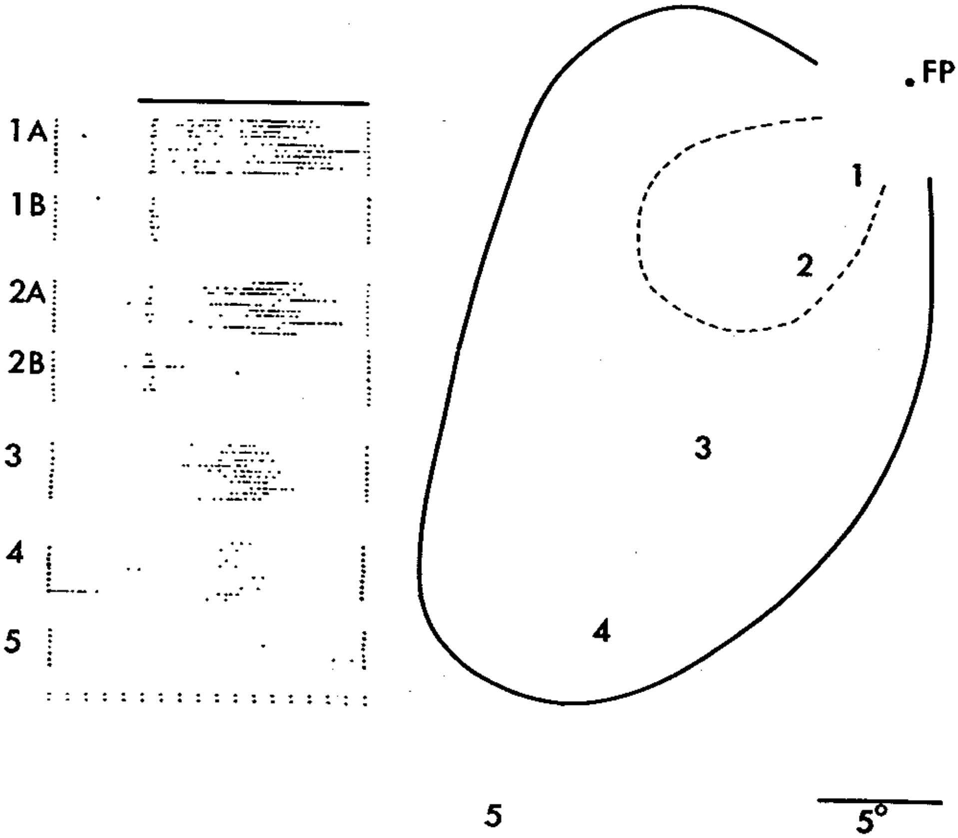

Fig. 6. Cell with movement field and visual receptive field. The movement field outlines the area where eye movements from the fixation point (*FP*) to another point were preceded by an increase in rate of cell discharges. Samples of these discharges to the points located on the diagram are shown in the dot patterns in *1A*, *2A*, *3*, *4*, and *5*. The eye movement followed onset of the stimulus spot target (*solid line above dot pattern*) by 200 to 300 msec. The *dashed line* outlines the receptive-field area of the same cell which was mapped by finding the response of the cell to small stationary spots of light at various points. This was done when the monkey was not saccading to the spots and sample records are shown in *1B* and *2B*. Other cells in the intermediate layers had receptive fields larger than the movement fields or no movement fields at all. (From Wurtz and Goldberg: J. Neurophysiol. 35: June-July, 1972.[24])

countered in the intermediate layers but less common for cells lying deeper in these intermediate layers.

The large size of the movement fields resembles the size of the larger sensory fields in the superficial layers and contrasts with the fine accuracy of eye movement guidance required for the monkey's oculomotor system. For example, a monkey can make an eye movement 20 degrees long with an error of less than 0.5 degree,[3] but the movement fields 20 degrees away from the fixation point were nearly an order of magnitude larger than 0.5 degree. It is impossible that single collicular cells could guide an eye movement accurately (as opposed to single oculomotor nuclear cells, which do transmit precise information about eye movement and velocity).[13] However, ensembles of these cells could transmit information fine enough for guidance that our analysis of single cell discharge patterns would miss.

Effect of collicular ablations on eye movements

In order to see the contribution of ensembles of collicular cells to the generation of accurate eye movement, we tested the effect of focal lesions in the colliculus on visually guided eye movements. Cells in each area of the colliculus are dedicated to a particular area of the visual field, both in responding to visual stimuli from that area and in discharging before eye movements to that area. We reasoned that a lesion made through a microelectrode from which we had recorded cells responsive to a particular area of the visual field should affect eye movements to that area of the field, and the nature of the deficit would help us describe the nature of the participation of the colliculus, if any, in the generation of eye movements.

In these experiments the receptive fields of cells on a penetration through the colliculus were first determined. Then the monkey saccaded to points in and around that area of the contralateral visual field where the receptive fields were found; saccades were also made to symmetrical points in the ipsilateral visual field. For example, Fig. 7, *A* shows the first three saccades to one point in the ipsilateral visual field in the upper three traces, and *B* shows the three saccades to the symmetrical point in the contralateral visual field in the lower three traces. Next a lesion was made by passing current through the microelectrode; the lesion invaded superficial and deeper layers but was almost exclusively limited to the superior colliculus (Fig. 8). Then, following the lesion and on subsequent days, we tested the monkey's ability to saccade to the area of the visual field where the receptive fields and movement fields of the destroyed cells were located. On the day following the lesion, the monkey saccaded to the ipsilateral area (Fig. 7, *B, top three traces*) and to the contralateral area (Fig. 7, *B, bottom three traces*) just as accurately as before the lesion. What did change was the latency of the saccades; they were now 150 to 300 msec. later when made to the area of the visual field related to the lesion.

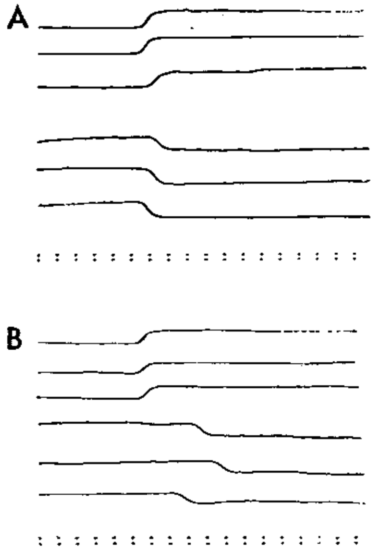

Fig. 7. Increased latency for saccades to a point in the contralateral visual field area where cells damaged by a focal lesion had their receptive fields. Top three traces in *A* (made before the lesion) and *B* (made the day after the lesion shown in Fig. 8) are to ipsilateral side; lower three traces are the contralateral side. Horizontal EOG records to a point ten degrees over and five degrees down on ipsilateral or contralateral side show an increased latency to contralateral point, no change to the ipsilateral point. (From Wurtz and Goldberg: J. Neurophysiol. **35**: June-July, 1972.[25])

This increase in latency with no detectable loss in accuracy has been found in two monkeys with lesions made by microelectrode in the colliculus, and in both monkeys the increase in latency has been associated with an area of the visual field approximately the same as that of the receptive fields mapped before the lesion was made. The identical effect has also been observed in two monkeys with large unilateral lesions in the colliculus; there was no loss in the accuracy of the eye movement, only a delay in initiating the saccade to the contralateral visual field. In the case of these unilateral lesions, the increased latency was related to all parts of the contralateral field.

Conclusion

These data indicate that the superior colliculus probably is not critical for eye movement guidance. The cell properties are not those of a precise guidance system (or

Fig. 8. Lesion in the superior colliculus made with the macroelectrode. Coronal sections are cresyl violet stained. Lesion was confined to superior colliculus except for slight damage to the hippocampus. (From Wurtz and Goldberg: J. Neurophysiol. 35: June-July, 1972.[25])

"foveator")[15] and the effect of ablating the colliculus is not to alter the accuracy or speed of an eye movement but only to increase reaction time for the eye movement. Instead, the results of our experiments suggest that the superior colliculus of the primate may contribute to a shift of visual attention and a facilitation of eye movement toward important areas of the visual field.

When an awake monkey shifts fixation from one point in the visual field to another, we can assume that he is shifting his attention from one point to another. Since the eye movements are by no means random, we can assume that the shift of attention precedes the shift of eye position, and, indeed, the purpose of this shift in gaze is to examine more carefully the stimulus that has attracted the shift of attention. The cells in the superficial layers show evidence of this shift in attention; they discharge more vigorously and more regularly to a stimulus the monkey is required to saccade to. The effect of this selective enhancement of discharge would be that stimuli in one part of the visual field are more effective than those falling on the rest of the retinal mosaic. Cells participating in this shift of attention from one part of the visual field to another need not be very precise analyzers of stimulus characteristics. Indeed, the collicular cells can specify only in a rough way where the important area of the visual field is. Similarly, the output of the movement-related cells in the intermediate layers could facilitate an eye movement to a general area of the field that could be translated into a precisely guided eye movement by other systems. When the collicular cells are destroyed by a lesion, we view the increased latency for a saccade as a delay in the monkey's noticing the target, so that the monkey shifts his attention to it more slowly and saccades to it later. The deficit following a collicular ablation is therefore a deficit in the transfer of the effect of visual attention to the oculomotor system, not a deficit in the guidance system itself.

We therefore see the shifting of attention and the facilitating of movement within the visual field as one important role for the primate superior colliculus. This more subtle but important function is in turn consistent with the lack of eye movement deficit following massive collicular lesions in monkeys[1, 12] as well as the blank stare and paucity of eye movements seen in such monkeys. The deficit in ability to shift attention we see in our lesioned monkeys is also similar to the attention deficit seen in cats with collicular lesions[19] and in a more subtle way parallels the global deficit of orientation seen by Schneider[16] in hamsters with collicular lesions.

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