

Single-Unit Recording and Stimulation in Superior Colliculus of the Alert Rhesus Monkey

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RECENT SINGLE-UNIT recording studies of the alert rhesus monkey superior colliculus have disclosed that the deeper layers of this structure contain cells which discharge in association with eye movement (15-17, 23, 24). Such units fire selectively prior to saccades of a specific direction and size, irrespective of the position of the eye in orbit.

Stimulation studies of the superior colliculus have so far produced conflicting results. Some reports suggest that in the alert cat stimulation brings the eye to a certain position in orbit irrespective of eye position prior to stimulation (1, 9, 19). Thus, the size and direction of elicited saccades is reported to vary as a function of initial eye position.

By contrast, in the alert monkey it has recently been reported that stimulation produces conjugate saccades of a specific size and direction; these parameters are the same no matter where the eye is in the orbit prior to stimulation (12, 15, 16). The stimulation map of Robinson (12) shows a reasonable correspondence with the receptive-field map of the superior colliculus reported by Cynader and Berman (5).

The aim of this study was to clarify the relationship between recording and stimulation data by using methods which allow a direct comparison. We used alert rhesus monkeys which had one eye immobilized for the mapping of visual receptive fields. The other eye was normal, thus permitting the study of eye movement. Stimulation and recording were carried out using the same low-resistance microelectrode; for each site sampled, records were obtained for both single-unit activity and for electrical stimulation.

METHODS

The experiment was carried out on four rhesus monkeys. For three of the animals the methods were similar to those described by Schiller and Koerner (17). One eye of each monkey was immobilized by transection of the 3rd, 4th, and 6th cranial nerves; d-c eye-movement electrodes were implanted around the orbit of the moving eye. A set of four screws, for subsequent securing of the head, and two adjustable ball-and-socket joints, with stainless steel tubes aimed at the superior colliculi, were implanted on the skull (details in ref 17). Placement of the tubes also permitted access to the abducens nucleus. In the fourth monkey we did not immobilize the eye. In this animal the effects of stimulation on conjugate eye movements were examined.

During the recording-stimulation experiments, the animal's head was secured using the skull screws (7). The fovea of the immobilized eye was mapped onto a tangent screen facing the animal. Unit activity, stimulation marker, and eye-movement activity were recorded on magnetic tape and were displayed on a multichannel stripchart recorder (Visicorder). Eye-movement calibration was carried out in a manner previously described (14).

The general procedure in this study entailed the lowering of the microelectrode into the superior colliculus, recording the activity of single units and mapping their receptive fields, and then stimulating the recording site through the same microelectrode. In the superficial layers primary emphasis was placed on locating receptive fields relative to the fovea and then determining the size and direction of saccades elicited by electrical stimulation. In the lower layers, where one encounters cells related to eye movement, a comparison was made between the "motor fields" (see Schiller and Koerner, ref 17) obtained with single units and with electrical stimulation.

Glass-coated platinum-iridium microelectrodes

were used (21). We found that passing 200- μ a, .5-msec pulses at 500 Hz produced no discernible damage to these electrodes. Since the range of stimulation was generally between 1 and 150 μ a, we could use these electrodes repeatedly without affecting the quality of the recording. In the three monkeys with immobilized eyes, 59 penetrations were made into the colliculi and 4 into the abducens nuclei. In the fourth monkey 10 sites were stimulated.

At the termination of the experiments animals were sacrificed and the recording sites were verified histologically.

RESULTS

Single-unit recording

The results of the recording data of this study are similar to those we have already reported (17). In the superficial layers (strata griseum superficiale and opticum), units appeared to respond only to visual stimuli. They showed neither directional selectivity nor orientational specificity. Unit discharge was independent of the sign of contrast; thus, flashing stimuli elicited both on- and off-bursts. The most effective stimulus was a moving one; responses could be obtained over a broad range of stimulus velocities. Generally, stimuli smaller than the size of the receptive field elicited the greatest number of discharges; large spots or diffuse light were quite ineffective in driving the unit.

As the electrode descended more deeply into the colliculus, the properties of light-driven cells changed in a rather subtle fashion. Cells no longer responded to smoothly moving stimuli. Instead, the best response was obtained either to flashes or to rapid, jerky stimulus displacements.

In the lower layers (strata griseum intermediale, and griseum profundum) of the superior colliculus, cells related to eye movement predominated. Typically, they began

their discharge 50–200 msec prior to a saccade, increased in frequency until the onset of the saccade, and then rapidly terminated their firing. Unit discharge was specifically associated with saccades of a particular size and direction, independent of initial eye position. The size of the motor fields (the range of saccade sizes and directions associated with a single unit) varied, primarily as a function of retinal eccentricity. The smallest fields we found were about 3° in diameter, the largest about 25°.

Eye-movement units appeared to be tuned; the response was most vigorous with saccades going to the center of the motor field. The majority of these units had a dual property; not only did they fire in association with certain saccades, but they also had visual receptive fields, which when stimulated with flashed or jerkily moving stimuli would, albeit weakly and erratically, produce a response. The receptive fields of such units were located prior to eye movement in that part of the visual field to which the fovea was directed by the saccade, which was associated with unit activity. Units with this dual property had practically no spontaneous activity.

Advancing the electrode past the region where these cells were located we observed a further subtle change. Units fired in association with saccades of specific sizes and directions, but they had a relatively high spontaneous activity and they did not appear to have visual receptive fields.

Many of the cells related to eye movement also responded during optokinetic and vestibular nystagmus. Figure 1 shows this. Optokinetic nystagmus was elicited with moving black and white stripes. Vestibular nystagmus was produced by irrigating the outer ear with cold water. Under such

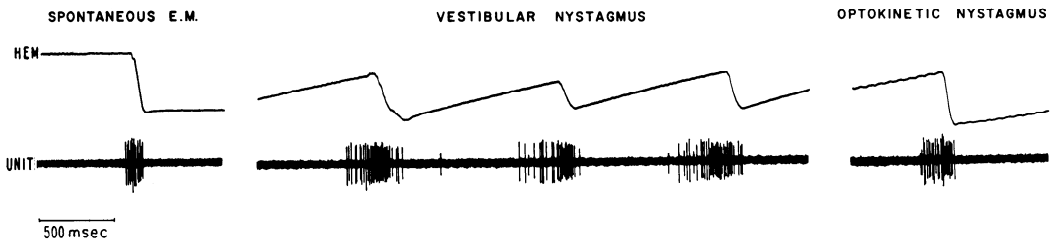


FIG. 1. Discharge characteristics of a cell in the deeper layers of superior colliculus. Discharge occurs prior to spontaneous saccades and prior to the fast phase of vestibular and optokinetic nystagmus. Records of the vestibular nystagmus were obtained in the dark.

conditions the size and direction of saccades was still a critical factor; unit firing occurred both in the light and in total darkness, but only with appropriate saccades.

Only a portion of the units tested discharged in association with vestibular nystagmus. It is difficult to state unequivocally whether those units which were silent failed to discharge because the size and direction of the fast phase was inappropriate or because these units are unresponsive during any kind of vestibular nystagmus. Because of this problem no meaningful statement can be made regarding the percentage of units which may be activated during vestibular nystagmus. However, both kinds of eye-movement units, those which had visual receptive fields and those which did not, could be driven with optokinetic and vestibular nystagmus.

Stimulation

In order to clarify eye-movement response characteristics to electrical stimulation, we compared the effect of such stimulation in the superior colliculus with that in the abducens nucleus.

The results of such a comparison are shown in Fig. 2. Stimulation of the abducens nucleus showed the size of the elicited eye movement to be a function of both the

duration and frequency of the stimulus train; the longer the duration and higher the frequency (up to 600 Hz), the larger and faster the eye movement. Response latency was 10–15 msec.

By contrast, stimulation of the superior colliculus produced very different effects. Differing frequencies between 150 and 600 Hz brought about no observable change in the direction, size, or velocity of the elicited saccade. The same was true for stimulus-train duration; saccade parameters remained unaffected. However, when train duration exceeded about 150 msec, we could see an interesting new effect. Instead of one saccade we now saw two, with an intervening fixation. Increasing stimulus duration further produced additional saccades with intervening fixations. The eye moved in a series of machinelike steps. Each saccade was of the same size and direction. The initial response occurred 20–30 msec after the onset of stimulation.

The effects described so far were observed in all layers of the colliculus. However, the current threshold for eliciting an eye movement changed quite notably as a function of depth of the penetration, decreasing with depth down to the level of the eye-movement cells. At this level threshold was at its minimum, being between 1

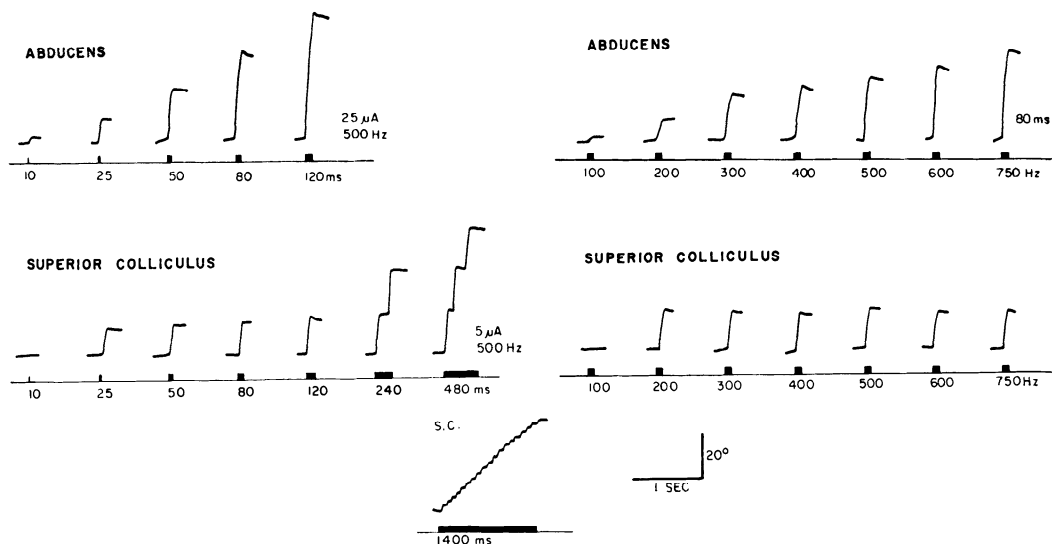


FIG. 2. Effects of electrical stimulation in the abducens nucleus and the superior colliculus as a function of burst duration and frequency. The long staircase of saccades shown at the bottom of the figure was elicited by stimulating within the anterior tip of the superior colliculus. All eye-movement records are horizontal with saccades going to the left.

and 5% of the threshold at the collicular surface. Deeper than this level, threshold increased. For short bursts, increasing stimulating current from threshold to 5 times threshold or more produced no noticeable change in the size and direction of saccades at any site. With long bursts of stimulation, however, the number of saccades increased to some extent (with an accompanying decrease in the duration of the intersaccade fixations) as a function of stimulus intensity. This too was found to be the case throughout the colliculus.

Stimulating the superior colliculus in the monkey with normal eyes always produced conjugate saccades. In all other respects the response characteristics were the same. Low-velocity eye movement analogous to smooth pursuit was never elicited successfully in any of the monkeys, even when the frequency was varied during the stimulus train.

Thus, it appears that the noted dimensions of saccades were unaffected by the parameters of electrical stimulation in the superior colliculus. The elicited saccades were also relatively independent of the position of the eye in the orbit prior to stimulation. This is shown in Fig. 3.

Some variability in the direction and size of the saccades can be observed in Fig. 3. Part of this may be due to lack of linearity in the eye-movement recordings at extreme

eye positions. To determine better the variability of the actual eye movement, we stimulated at four collicular sites a large number of times, initiating the stimulation only when the animal was looking within 10° of straight ahead. This way we were within the range of linearity of our recording system.

The distribution of saccade sizes and directions for one stimulated site ($11 \mu\text{a}$) is shown in Fig. 4. The mean saccade size for this site was 7.2° with a standard deviation of 1.1° . The direction of the saccade was to the left having a mean angle of 99.1° and a standard deviation of 9.1° , where up = 0° , left = 90° , down = 180° , and right = 270° . At the three other sites stimulated in this fashion mean saccade sizes were $3.1 \pm 1.0^\circ$ sd, $8.7 \pm .96^\circ$ sd, and $27 \pm 3.4^\circ$ sd.

At 18 other sites 20 or more stimulus trains were delivered with the eye in random initial positions. Because of nonlinearities in the eye-movement recording system at extreme eye positions, this technique may somewhat overestimate the variability of elicited saccades. However, the technique does provide an upper limit to this variability. For each site the following statistics were calculated: mean saccade length, standard deviation of saccade length, and standard deviation of saccade direction. No systematic difference was found between superficial and deep sites in these measures of variability. Standard deviation of saccade length showed a tendency to increase with saccade length (Pearson's product-moment correlation coefficient $r = .685$, significant $P < .001$ by Fisher's z transform). Thus, for the 11 sites with mean saccades smaller than 13° (range: 4.1 – 12.9°), standard deviation of saccade length ranged from $.7$ to 2.6° (median = 1.7°); for the 7 sites with mean saccades greater than 13° (range: 13.8 – 27°), standard deviation of saccade length ranged from 2.3 to 5.0° (median = 3.7°). Standard deviation of saccade direction ranged from 5.6 to 21.0° (median = 9.9°) and showed no significant relation to mean saccade length or direction.

We found, in agreement with Robinson (12), that the only determinant of the size and direction of elicited saccades was the site of stimulation. In the anterior part of

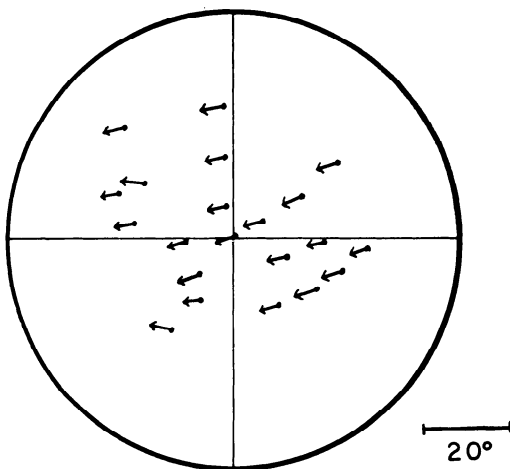


FIG. 3. Saccades elicited by stimulation of a single site of the superior colliculus. Dot shows initial eye position. Arrow shows size and direction of saccade produced by the stimulation.

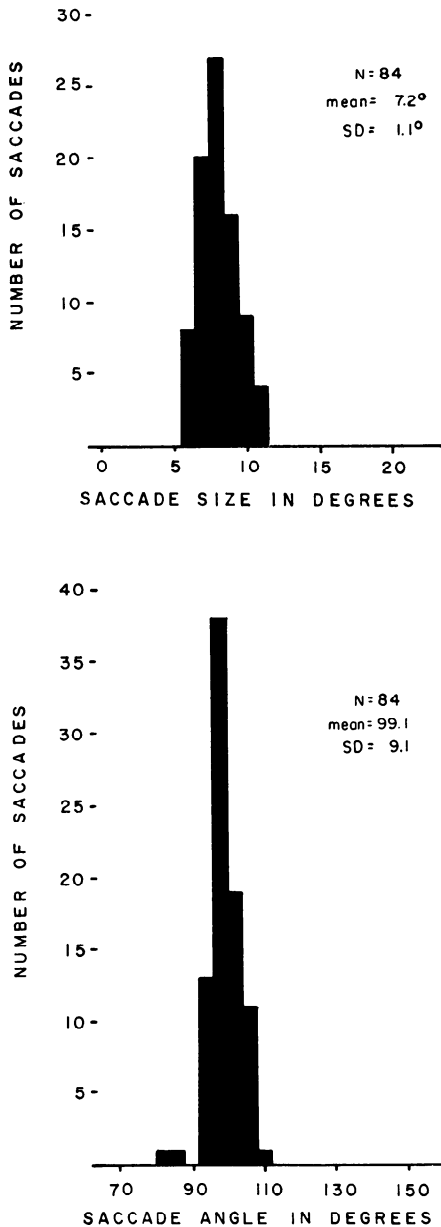


FIG. 4. Distribution of saccade sizes and directions obtained by repeated stimulation of one site in the superior colliculus. Saccade-size distribution is shown above; saccade direction is below (where 0° = up, 90° = left, 180° = down, and 270° = right).

the colliculus stimulation produced small saccades and in the posterior part, large ones. Medial stimulation results in an upward saccade and lateral stimulation a downward movement. This relationship suggests a close correspondence with the visual

map (5). In the next section this correspondence is examined more closely.

Comparisons between stimulation and recording

SUPERFICIAL LAYERS. In the superficial layers we first determined the location of the receptive field of each unit and then stimulated at the same site. For stimulation we routinely employed a 70-msec train of .5-msec rectangular cathodal pulses at 300 Hz; all thresholds stated are for this pulse configuration. Threshold for eliciting an eye movement in the superficial layers decreased from a range of $150\text{--}400\ \mu\text{a}$ at the surface to about $15\ \mu\text{a}$. The mean elicited saccade size and direction were determined on the basis of 8–14 repeated stimulus trains. Eye-movement calibration was obtained using a perimeter with peepholes (14) and was done immediately after stimulating. The basic relationship between stimulation and recording is shown for 14 sites in Fig. 5.

Of a total of 43 sites studied in this manner in two animals, complete data were gathered at 28. For these 28 sites the correspondence between visual receptive fields (median diameter 4.8°) and the saccades elicited by electrical stimulation (all at less than $150\ \mu\text{a}$) was assessed from plots like Fig. 5. The termination of the mean saccade at these 28 sites fell at a median distance of 2° visual angle ($\pm 2^\circ$ interquartile range) from the receptive-field center; in 72% of the cases this was inside the receptive field. The distribution of the saccades around the receptive-field centers was random. For the 15 sites in two animals at which saccades were elicited with less than $30\ \mu\text{a}$, the correspondence between stimulation and recording was even better; the mean saccade fell at a median distance of 1° ($\pm 1^\circ$ interquartile range) from the receptive-field center.

DEEPER LAYERS. As one progressed to the deeper layers of the superior colliculus, the stimulating-current threshold for eliciting saccades dropped dramatically. In the region previously identified as having primarily visual cells which responded to jerky stimulus displacement, the stimulation threshold for eliciting a saccade was $15\text{--}30\ \mu\text{a}$. Once the region was reached where eye-

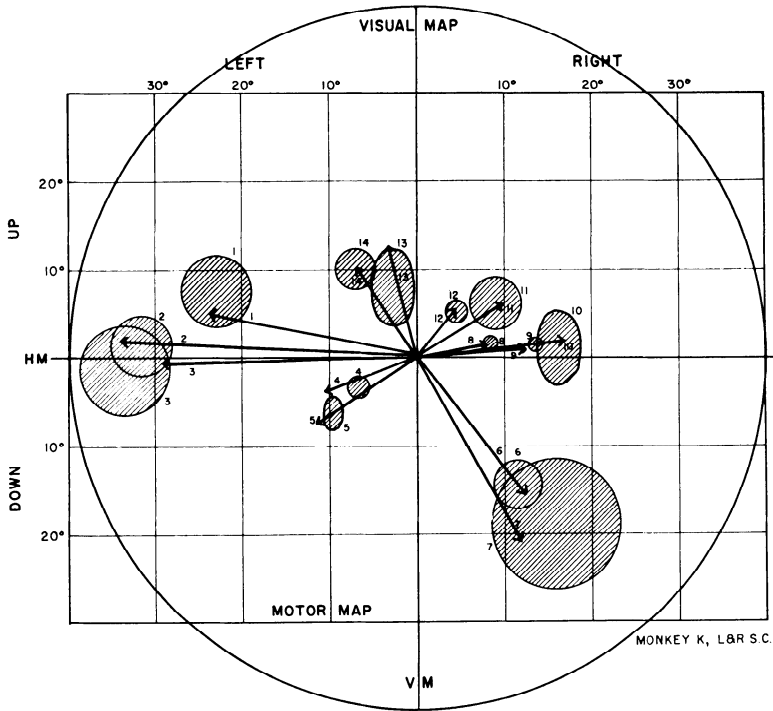


FIG. 5. Effects of recording and stimulation in the superficial layers of the superior colliculus. The visual map with the receptive fields of 14 units is superimposed on the motor map with its arrows representing the electrically elicited saccades at each of the 14 sites. The length of each arrow represents the mean length of 8-14 stimulation-elicited saccades; the direction of each arrow represents the mean direction of saccades. HM = horizontal meridian, VM = vertical meridian.

movement cells predominate, the threshold went down to 1-9 μ a. The current passed at these low levels appeared to produce little if any damage, since one could almost invariably record from the same unit after stimulation.

Figure 6 shows records from a typical unit related to eye movement in the superior colliculus, the effects of electrical stimulation at that site, and the response of the same unit after stimulation.

To assess the relationship between unit activity and stimulation, "motor maps" were drawn for a total of 30 recording

sites. These maps were obtained by taking long strips of recording and stimulation data. The size and direction of each saccade was measured and plotted, and its relationship to unit activity or stimulation assessed. A typical map of this sort is shown in Fig. 7. A very close relationship was found; for all 30 sites studied in this manner, the fields established by stimulation were almost completely enclosed by the fields established by recording.

DISCUSSION

The results of this study show a close correspondence between single-unit recording and electrical stimulation in the superior colliculus. In the superficial layers electrical stimulation elicited saccades which brought the foveal projection onto that part of the visual field occupied by the receptive field of the unit prior to the initiation of movement. In the deeper layers the motor fields obtained by stimulation and by recording were in the same region.

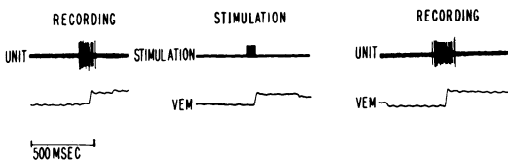


FIG. 6. Recording and stimulation at one site in the deeper layers of the superior colliculus. Saccade-associated unit burst is shown before and after electrical stimulation.

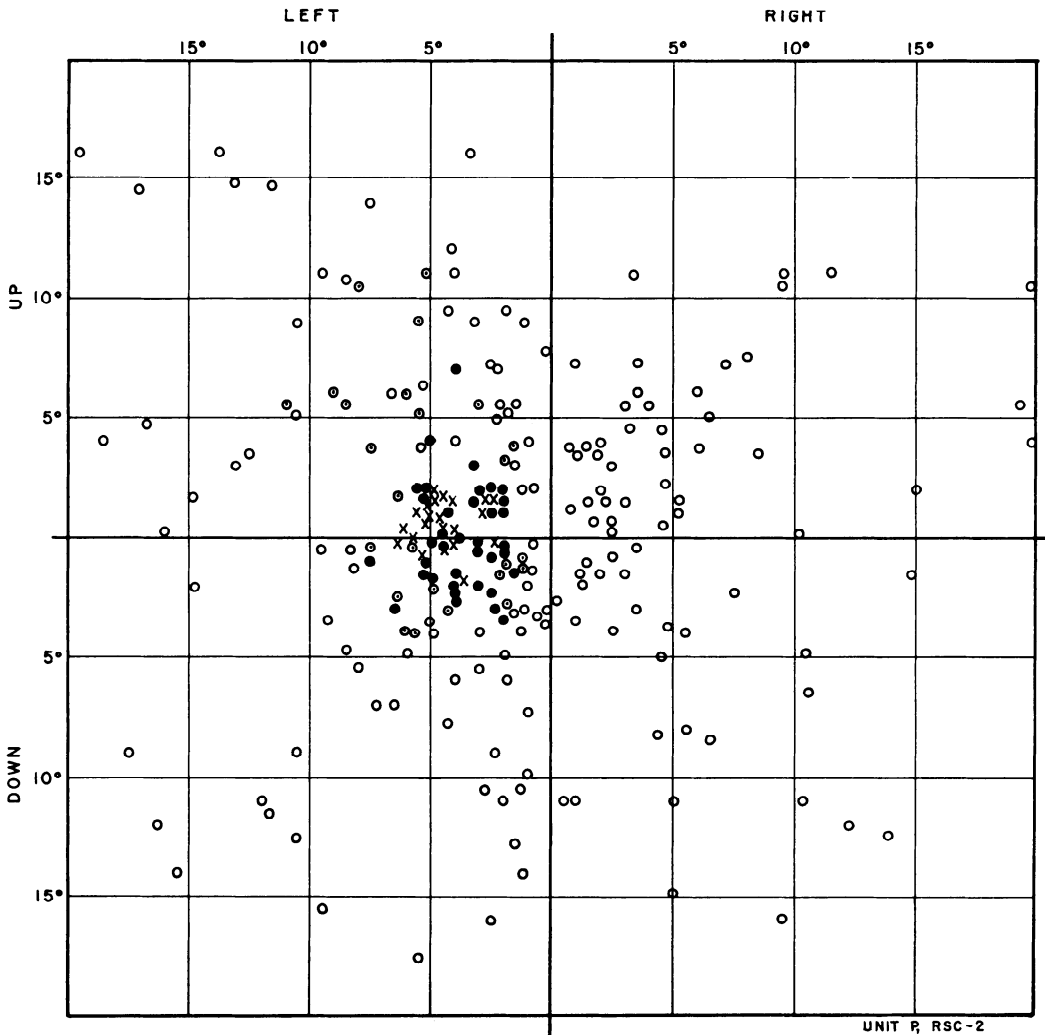


FIG. 7. Motor map obtained with recording and stimulation in one collicular site. Open circles show spontaneous saccades not associated with unit activity. Filled circles represent saccades associated with unit activity. Dotted circles represent saccades associated with weak unit discharge. Saccades elicited by stimulation are shown by \times .

In a recent study Goldberg and Wurtz (8) reported that in the superficial layers (strata griseum superficiale and opticum), some of the units show an enhanced discharge to a visual stimulus when a saccade toward that stimulus follows. Since our monkeys were not trained, we were unable to observe this interesting effect. In our situation eye-movement-associated bursts in these two layers occurred only after saccades in light, probably as a result of the shift of visual patterns on the retina, and did not occur at all in darkness. In the lower layers (strata griseum intermediale, album inter-

mediale, and griseum profundum) the eye-movement-related properties of units became distinct in that they discharged prior to certain saccades. Eye-movement-related discharge occurred in light even in the absence of any preceding change in visual pattern and for many of these units was also demonstrable in darkness. We previously reported that a high percentage of these eye-movement units have visual receptive fields (17). Our subsequent work, including this report, showed a similar ratio for the more superficial eye-movement units and also disclosed the deeper type of eye-

movement units with higher spontaneous activity which do not appear to have visual receptive fields. Wurtz and Goldberg (23, 24) obtained a lower overall percentage of eye-movement units with visual receptive fields. This slight discrepancy may reflect differences in sampling or in preparation. With the immobilized eye we may have been able to spend more time searching for visual receptive fields, which for many of these units were hard to find because the units' discharge to visual stimulation was frequently weak and erratic.

Asanuma and his collaborators (2, 18) have recently reported eliciting motor responses by stimulation of motor cortex with currents of similar magnitude to those we employ in the colliculus. Their measurements indicate that 5- μ a, .2-msec cathodal pulses (equivalent by the strength-duration relation of Stoney et al. (18) to 3 μ a of the .5-msec pulses we employ) directly excite cortical cells within about 65 μ m of the electrode tip (18). Furthermore, short pulse trains at this level of stimulation, which produced motor effects with the electrode in gray matter, never produced motor effects when the electrode was pushed into white matter, suggesting that this level of stimulation was virtually ineffective to fibers (2). There are cytoarchitectural differences between motor cortex and colliculus. Further, there are differences between the pulse configurations employed in the current study and those of Asanuma et al. (2). Despite these differences, however, the fact that the threshold for eliciting an eye movement was commonly less than 3 μ a when the electrode tip was in the region of the eye-movement units suggests that collicular stimulation may produce its effect by excitation of the eye-movement units.

The findings reported here suggested to us the possibility that the superior colliculus plays a role in mechanisms involved in foveation. In addition to the basic correspondence between stimulation and recording data, there are the very low thresholds and high-command value of stimulation, as indicated by the immediacy and consistency of the response. The fact that the size and direction of the saccades do not depend on initial eye position in orbit, as shown also by long-duration stimulation

which elicits a staircase of repeated saccades each having the same size and direction, clearly indicates a coding relative to the fovea.

Two problems exist regarding the foveation hypothesis. One is that the accuracy of oculomotor target acquisition in the monkey appears much greater than one would expect on the basis of the size of both the receptive fields and the motor fields of eye-movement units. While collicular visual receptive fields are very small near the fovea, sometimes only $1/8^\circ$ in diameter, field size rapidly increases as a function of retinal eccentricity; 20-30° from the fovea field sizes of 10° or more are common even though the optimal stimulus within the field may only be 3-5°. The motor fields of the lower layers show a similar pattern. Fields associated with small saccades may be 3-4° in diameter, while fields associated with large saccades may be as much as 15-25° in diameter. By contrast, we found that monkeys trained to acquire visual targets with saccadic eye movements show a standard deviation of 1.6° for the length of the initial saccade to an actual target when this target appears 10° from the fixation point.

Several observations mitigate the discrepancy between the size of the eye-movement units' motor fields and the accuracy of primate target acquisition. One is that eye-movement units appear to be tuned (17, 24). A more vigorous unit discharge is obtained to saccades going to the center of the motor field than to its periphery. This may further be sharpened by the collective action of numerous units within a given area. Moreover, our data from repeated stimulation show a narrow distribution of saccade sizes and directions (Fig. 4), which compares favorably with the noted behavioral data.

The second problem regarding the foveation hypothesis has to do with the findings of lesion studies in monkeys. Pasik, Pasik, and Bender (11) claimed no deficit in eye movement as a result of colliculus ablation. Compelling support for this position comes from the recent work of Wurtz and Goldberg (25); they also failed to find deficits in the accuracy of target acquisition after colliculus lesions, although they did note an increase in the latency of the saccadic re-

sponse. By contrast, Denny-Brown (6) found extensive deficits in eye movement and other coordinated motor acts after colliclectomy. In our hands conflicting results have been obtained. Monkeys show a definite eye-movement deficit immediately after ablation. Subsequently, however, some of them recover completely over a period of a few weeks or months, while others fail to do so.

Thus, the ablation data do not provide ready support for a foveation hypothesis. However, it is expected that, like most functions, this one may be multiply represented, permitting other brain structures to contribute to it.

In line with this observation is the fact that the superior colliculus is not the only structure from which stimulation elicits saccades of specific sizes and directions irrespective of stimulation parameters and initial eye position. Similar effects have been reported for the frontal eye fields (13) and for visual cortex (15, 16). In both of these structures, the current levels needed to elicit eye movements are much greater (frontal eye fields 40–1,500 μ a, visual cortex 200–2,000 μ a). In addition, the correspondence between unit data and stimulation is poor in both of these regions. This may be due to current spread in visual cortex, but in the frontal eye field the situation is even more obscure, as can be seen by comparing the data of Robinson and Fuchs (13) with those of Bizzi and Schiller (4). Nevertheless, these three structures seem definitely to be involved in some aspects of eye movement, although the nature of the contributions made by each structure and their interrelations remain to be specified.

Two additional hypotheses regarding collicular function have currently been advanced. Wurtz and Goldberg (23, 25) proposed that the superior colliculus could serve the function of alerting the organism to stimuli in the visual field. Such a hypothesis does not require the motor field specificity the foveation hypothesis necessitates. Wurtz and Goldberg's finding of increased saccade latency without an accompanying deficit in the accuracy of target acquisition may be seen as favoring this view. However, we know of no direct evidence available at this time to decide between the

foveation and the alerting or attention hypotheses.

A third hypothesis proposes that the colliculus is involved in corollary activity (10, 20). Two versions of this hypothesis may be noted. One proposes a mechanism requiring only an indication that an eye movement is going to occur (22). The colliculus would seem far too elaborate a structure to carry out such a simple task. A second version of a corollary hypothesis requires the specification of an impending eye movement in terms of a coordinate system stating to what position in orbit the eye will move (19). The corollary discharge is believed, in this context, to serve the function of indicating the location of the eye in orbit, thereby enabling proper orientation toward objects in space. The superior colliculus of the monkey would seem to be ill suited for this task, since it does not appear to code any eye-orbit relationship.

SUMMARY

1. The superior colliculus of alert rhesus monkeys was investigated. One eye of each animal was immobilized by transection of the 3rd, 4th, and 6th cranial nerves. The location of receptive fields of single units, their properties, and relation of unit discharge to eye movement were studied at various depths within the superior colliculus. Following recording at each site electrical stimulation was delivered through the same microelectrode and the resulting eye movement was compared with the recording data.

2. The recording data show, in agreement with previous reports, that in the superficial layers units appear to respond exclusively to visual stimuli. In the deeper layers cells related to eye movement predominate. The latter discharge prior to saccades of a specific size and direction.

3. Stimulation of the superior colliculus elicits saccades of particular angular extents and directions that are relatively independent of stimulation parameters and are determined by the site of stimulation. Threshold for eliciting saccades drops from 400 μ a in the superficial layer to as low as 1 μ a in the deeper layers of the colliculus. Prolonged stimulation elicits a staircase of identical saccades.

4. A close correspondence was obtained between recording and stimulation data. In the superficial layers the size and direction of elicited saccades were such as to bring the foveal projection onto that part of the visual field occupied by the receptive field prior to the initiation of movement.

5. In the deeper layers, stimulation produced saccades which duplicated the characteristics of the spontaneous saccades specifically associated with unit discharge. At each site the motor maps defined by the dis-

charge of single units enclosed those obtained by stimulation.

6. The data are discussed in relation to three hypotheses about collicular function; foveation, orientating (i.e., shifting of attention), and corollary discharge.

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REFERENCES

1. APTER, J. T. Eye movements following strychninization of the superior colliculus of cats. *J. Neurophysiol.* 9: 73-86, 1946.
2. ASANUMA, H. AND ROSEN, I. Topographical organization of cortical efferent zones projecting to distal forelimb muscles in the monkey. *Exptl. Brain Res.* 14: 243-256, 1972.
3. BIZZI, E. Discharge of frontal eye field neurons during saccadic and following eye movements in unanesthetized monkeys. *Exptl. Brain Res.* 6: 69-80, 1968.
4. BIZZI, E. AND SCHILLER, P. Single unit activity in the frontal eye fields of unanesthetized monkeys during eye and head movement. *Exptl. Brain Res.* 10: 151-158, 1970.
5. CYNADER, M. AND BERMAN, N. Receptive-field organization of monkey superior colliculus. *J. Neurophysiol.* 35: 187-201, 1972.
6. DENNY-BROWN, D. The midbrain and motor integration. *Proc. Roy. Soc. Med.* 55: 527-538, 1962.
7. EVARTS, E. V. A technique for recording activity of subcortical neurons in moving animals. *Electroencephalog. Clin. Neurophysiol.* 24: 83-86, 1968.
8. GOLDBERG, M. E. AND WURTZ, R. H. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* 35: 560-574, 1972.
9. HYDE, J. E. Interrelationship of brainstem and cortical areas for conjugate ocular movements in cats. In: *The Oculomotor System*, edited by M. B. Bender. New York: Harper and Row, 1964.
10. JOHNSTONE, J. R. AND MARK, R. F. The efference copy neuron. *J. Exptl. Biol.* 54: 403-414, 1971.
11. PASIK, T., PASIK, P., AND BENDER, M. B. The superior colliculi and eye movements. *Arch Neurol.* 15: 420-436, 1966.
12. ROBINSON, D. A. Eye movements evoked by superior colliculus stimulation in the alert monkey. *Vision Res.* In press.
13. ROBINSON, D. A. AND FUCHS, A. F. Eye movements evoked by stimulation of frontal eye fields. *J. Neurophysiol.* 32: 637-648, 1969.
14. SCHILLER, P. H. The discharge characteristics of single units in the oculomotor and abducens nuclei of the unanesthetized monkey. *Exptl. Brain Res.* 10: 347-362, 1970.
15. SCHILLER, P. H. Some functional characteristics of the superior colliculus of the rhesus monkey. In: *Cerebral Control of Eye Movement and Motion Perception*, edited by J. Dichgans and E. Bizzi. Basel: Karger, 1972.
16. SCHILLER, P. H. The role of the monkey superior colliculus in eye movement and vision. *Invest. Ophthalmol.* 2: 451-460, 1972.
17. SCHILLER, P. H. AND KOERNER, F. Discharge characteristics of single units in superior colliculus of the alert rhesus monkey. *J. Neurophysiol.* 34: 920-936, 1971.
18. STONEY, S. D., JR., THOMPSON, W. D., AND ASANUMA, H. Excitation of pyramidal tract cells by intracortical microstimulation: Effective extent of stimulating current. *J. Neurophysiol.* 31: 659-669, 1967.
19. STRASCHILL, M. AND RIEGER, P. Optomotor integration in the colliculus of the cat. In: *Cerebral Control of Eye Movement and Motion Perception*, edited by J. Dichgans and E. Bizzi. Basel: Karger, 1972.
20. TEUBER, H.-L. Perception. In: *Handbook of Physiology. Neurophysiology*. Washington, D.C.: Am. Physiol. Soc. 1960, sect. 1, vol. III, chapt. 65, p. 1595-1668.
21. WOLBARSHIT, M. C., MACNICHOL, E. F., AND WAGNER, H. G. Glass insulated platinum microelectrode. *Science* 152: 1309-1310, 1960.
22. WURTZ, R. H. AND GOLDBERG, M. E. Superior colliculus cell responses related to eye movements in awake monkeys. *Science* 171: 82-84, 1971.
23. WURTZ, R. H. AND GOLDBERG, M. E. The role of the superior colliculus in visually evoked eye movement. In: *Cerebral Control of Eye Movement and Motion Perception*, edited by J. Dichgans and E. Bizzi. Basel: Karger, 1972.
24. WURTZ, R. H. AND GOLDBERG, M. E. Activity of superior colliculus in behaving monkey. III. Cells discharging before eye movements. *J. Neurophysiol.* 35: 575-586, 1972.
25. WURTZ, R. H. AND GOLDBERG, M. E. Activity of superior colliculus in behaving monkey. IV. Effects of lesions on eye movements. *J. Neurophysiol.* 35: 587-596, 1972.