

Eye and Head Movements Evoked by Electrical Stimulation of Monkey Superior Colliculus

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Received January 13, 1975

Summary. In unrestrained animals of many species, electrical stimulation at sites in the superior colliculus evokes motions of the head and eyes. Collicular stimulation in monkeys whose heads are rigidly fixed is known to elicit a saccade whose characteristics depend on the site stimulated and are largely independent of electrical stimulation parameters and initial eye position.

This study examined what role the colliculus plays in the coding of head movements. A secondary aim was to demonstrate the effects of such electrical stimulation parameters as pulse frequency and intensity. Rhesus monkeys were free to move their heads in the horizontal plane; head and eye movements were monitored. As in previous studies, eye movements evoked by collicular stimulation were of short latency, repeatable, had a definite electrical threshold, and did not depend on the initial position of the eye in the orbit. By contrast, evoked head movements were extremely variable in size and latency, had no definite electrical threshold, and did depend on initial eye position. Thus when the eyes approached positions of extreme deviation, a head movement in the same direction became more likely. These results suggest that the superior colliculus does not directly code head movements in the monkey.

Key words: Eye movement — Head movements — Eye-head coordination — Superior colliculus

Introduction

Studies by Akert (1949), Hess *et al.* (1946), Schaeffer (1972), Straschill and Rieger (1972) and others have shown that in unrestrained animals of many species electrical stimulation of the superior colliculus causes motions of the eyes and head resembling an orienting movement. In the freely moving animal it has been difficult to measure the evoked eye and head movements with precision, although a general relation between stimulation site on the colliculus and elicited movement has been established. Sites lateral in the colliculus yield movements contralateral and downward; medial sites yield contralateral upward motions. For equivalent stimulation posterior sites yield larger movements than anterior sites. This relationship appears to correspond with the topography of the visual field in the superficial layers of the colliculus, as established by Akert (1949), Apter (1946) and others.

In alert monkeys with restrained heads collicular stimulation elicits precise saccadic eye movements. Robinson (1972) and Schiller and Stryker (1972) have shown the size and direction of such eye movements to depend on the site of stimulation in the colliculus. The motor topography derived on the basis of the size and direction of elicited saccades at various sites in the superior colliculus (Robinson, 1972) matches the visual map of this structure demonstrated in paralyzed animals by Cynader and Berman (1972) using single-unit recording techniques.

In alert monkeys with one eye paralyzed, we found these two topographies to be in precise register: each brief stimulus train elicited a saccade of such size and direction that it brought the foveal projection onto that part of the visual field which had been occupied by the receptive fields of single cells at the stimulation site prior to the initiation of movement (Schiller and Stryker, 1972). The same was true of the eye-movement cells in the intermediate layers of the superior colliculus, as reported by Schiller and Koerner (1971), and Wurtz and Goldberg (1972). These cells have a visual receptive field and discharge specifically prior to saccades which bring the fovea onto the receptive fields of these units. Thus it appears that the oculomotor map of the monkey colliculus, like the sensory map, is coded in retinal coordinates.

These observations were made in monkeys with restrained heads. If the head is free to move, the relationship between visual targets and head and eye position becomes more complicated, in part because motion of the head activates the vestibular system which Morasso, Bizzi and Dichgans (1973) have shown to be closely coupled with the saccadic oculomotor system. Accordingly the first objective of the current study was to determine the effect of collicular stimulation in alert monkeys who were free to move their heads in the horizontal plane.

Initial work indicated that eye movements elicited by collicular stimulation were largely independent of the parameters of electrical stimulation (Robinson, 1972; Schiller and Stryker, 1972). We observed, however, that some parameters do produce certain alterations in the typical sequence of elicited eye movement. Therefore, a secondary object in this study was to determine to what extent the parameters of stimulus-train duration, intensity and pulse frequency affect elicited head and eye movements.

Methods

Stimulation and recording methods carried out on the three monkeys of this study were as previously described (Schiller and Stryker, 1972). One eye of each monkey was surgically immobilized. Four silver-silver-chloride electrodes were implanted around the orbit of the intact eye for d.c. electro-oculographic recording of eye movement. Microelectrodes for stimulation and recording were lowered into the superior colliculus through a tube held in a ball and socket chamber implanted on the skull. Electrical stimulation (0.5 msec cathodal pulses) was delivered through a Grass PSIU-6 photoelectric constant current stimulus isolation unit. The monkey's head was free to rotate in the horizontal plane, with the position of the head holder being monitored by a low-torque potentiometer (Bizzi and Schiller, 1970). Alternatively, the head holder could be fastened to remain in any desired position.

Because only horizontal head movements were possible, we restricted our stimulation to areas in the colliculus near the representation of the horizontal meridian. This was accomplished by plotting receptive fields for visually-driven units through the immobilized eye and by examining the eye movements evoked by stimulation. Sites where the elicited eye movement differed from horizontal by more than 10° were not considered for this study.

Results

Although the major aim of this study was to investigate combined movements of the head and eyes, new results on eye movements elicited by collicular stimulation during head restraint are presented first, in order to facilitate comparison with the situation in which the head is free to move.

1. Collicular Stimulation During Head Restraint

In this section we report the results obtained when the parameters of current-pulse intensity, pulse frequency, and pulse-train duration were systematically varied. The size and latency of the elicited eye movements constitute the basic data.

a) Brief Pulse Trains

Short pulse trains (<120 msec) evoked a single saccade. For such trains there was found to be a well-defined current threshold: with an increase of less than 30% in stimulating current, the probability of eliciting a saccade rose from near zero to near one. We took "threshold" to be the minimum intensity which was sufficient to evoke a saccade with almost every pulse train. Such thresholds could be determined reproducibly within 15% and were found to be within the range previously reported (1 to 400 μA for 70 msec trains of 0.5 msec cathodal pulses at 300 Hz using platinum-iridium microelectrodes). Threshold depended primarily on the layer of the colliculus in which the stimulating electrode was located and secondarily on the size of the stimulating electrode, being higher by a factor of five or more for large insect pin electrodes (1/2 to 1 mm exposed tip) than for microelectrodes (10 to 50 μm exposed tip).

For these short pulse trains, increasing the intensity from threshold to twice that value had no measurable effect on size and direction of the elicited saccade, but did shorten its latency from between 50 and 100 msec at threshold to a minimum of about 25 msec. Further increases, up to five times threshold, caused no further change in the elicited saccade.

b) Long Pulse Trains

Pulse trains whose durations were greater than about 200 msec elicited a series of approximately equal saccades separated by intervals of fixation. Such a series of saccades could frequently be elicited with 30% less current than the threshold for a 70 msec pulse train. For such long pulse trains the effects of intensity are illustrated in Fig. 1.

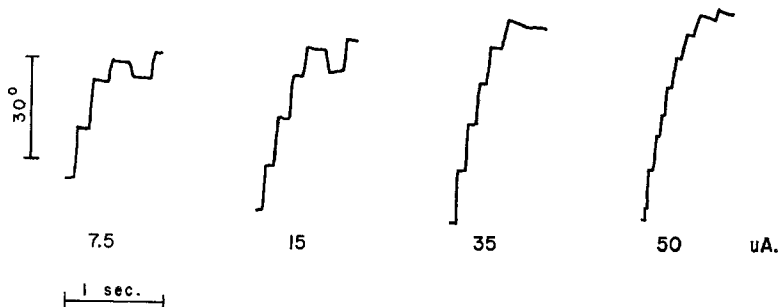


Fig. 1. Horizontal eye movements evoked from one collicular site by 1 sec stimulus trains (0.5 msec cathodal pulses at 300/sec) at the four different current intensities indicated

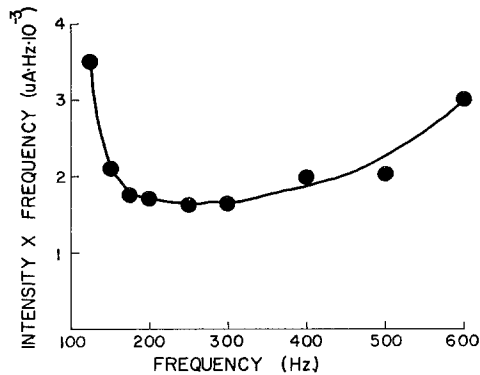


Fig. 2. Threshold current intensity for eliciting a saccade using 70 msec trains of 0.5 msec cathodal pulses at frequencies from 125 to 600 pulses/sec. Data are plotted as time-average cathodal current (= current per pulse times frequency) against frequency

With low-intensity stimulation, the saccades were very nearly equal while the intersaccadic fixation interval was long and somewhat variable (approximately 100 to 250 msec). In addition, occasional saccades in the opposite direction were interspersed, as if the monkey were capable of counteracting the effect of the stimulation. As the intensity of stimulation was increased two phenomena not previously reported were observed: 1. The intersaccadic fixation intervals became more regular and shorter, while saccades in the opposite direction were no longer seen during the pulse train. 2. At still higher intensities, the intersaccadic interval became shorter still, while the successive saccades, following the first one, became reduced in size but did not change direction. The minimum intersaccadic interval observed was 60 msec (at 50 μ A, $10 \times$ threshold).

In a few instances in which we stimulated with long pulse trains at more than ten times threshold, a smooth eye movement appeared, which was in the same direction as the staircase of saccades. Perhaps this smooth eye movement represents a discontinuous shortening of intersaccadic fixation interval to zero. Mere current spread to nearby oculomotor and premotor structures is an unlikely explanation, we think, because current spread would not necessarily evoke smooth eye movements in the same direction as the saccades. Because of the relatively high levels of stimulating current involved, we did not investigate this phenomenon systematically.

For both short and long stimulus trains, the parameter of pulse frequency was studied in a manner similar to current intensity. The effects of increasing frequency were similar to those of increasing current intensity: intersaccadic fixation intervals were shorter and successive saccades following the first were smaller. Such an apparent trade-off between frequency and current was investigated by determining current threshold at several sites with a number of different frequencies. Figure 2 shows results from one such site. The trade-off is very good between 175 and 400 Hz, with product of frequency and threshold intensity (= total stimulating current) remaining nearly constant. Outside this range of frequencies, a greater amount of total stimulating current was required.

2. Collicular Stimulation with the Head Unrestrained in Horizontal Plane

a) Brief Pulse Trains

Short-duration stimulating pulse trains (< 120 msec), which were sufficient to elicit only one saccade, were followed by head movements in the same direction only occasionally and with variable latency. The shortest latencies we observed were 90 msec. The probability of a head movement with these short trains was changed very little by increasing the stimulating current from the eye-movement threshold up to five times that threshold. However, stimulation at more posterior sites in the colliculus, which elicited larger saccades, was also more likely to elicit a head movement. At all sites studied in this fashion, the head movement was not seen to have any well-defined electrical threshold: it was never elicited reliably at the intensities we used, and variations of stimulating current on the order of a factor of five produced only small changes in the probability of a head movement. The probability of a head movement seemed to depend most strongly on the eye position following the elicited saccade. When the saccade brought the eye to positions of extreme deviation in orbit, a head movement was likely to follow.

Whenever the head moved, either spontaneously or in response to electrical stimulation, the eyes showed backward compensatory movements which matched the head movement in speed, but were in the opposite direction. These backward compensatory eye movements, which Bizzi and his co-workers (1970, 1971) have shown to be largely due to vestibular input, serving the function of stabilizing the gaze in space, were never disrupted during collicular stimulation.

b) Long Pulse Trains

Long pulse trains, which evoked a series of saccades, were much more effective at eliciting head movements. When the electrical stimulation was maintained long enough, a head movement would usually commence some time after the eyes had passed the midline, but such head movements were extremely variable in their time of onset, size and velocity. The best predictor of the time of onset of the head movement was the position of the eye in orbit. Figure 3 illustrates head and eye movements obtained from stimulation at one collicular site with the eyes starting at three different initial positions. As can be seen, the further the eye is displaced in orbit in the direction of its motion at the onset of stimulation, the shorter is the latency of the ensuing head movement. Figure 4 illustrates this relationship for 24 stimulus trains delivered at one collicular site. The considerable variability in head-movement latency is clear.

Suprathreshold variation in current intensity had an effect on combined movements of the eyes and head similar to its effects described above on eye movements in monkeys with fixed heads. The head-movement threshold was never less than the eye-movement threshold. Stimulation at the eye-movement threshold usually elicited a head movement if maintained long enough to bring the eyes to peripheral fixation. Near the eye-movement threshold, as described for monkeys with fixed heads, saccades in the opposite direction were sometimes interposed; in these cases usually no head movements were made. As the current was increased, these interposed saccades in the opposite direction were no longer present; with still higher intensities the duration of the fixation intervals between saccades decreased and

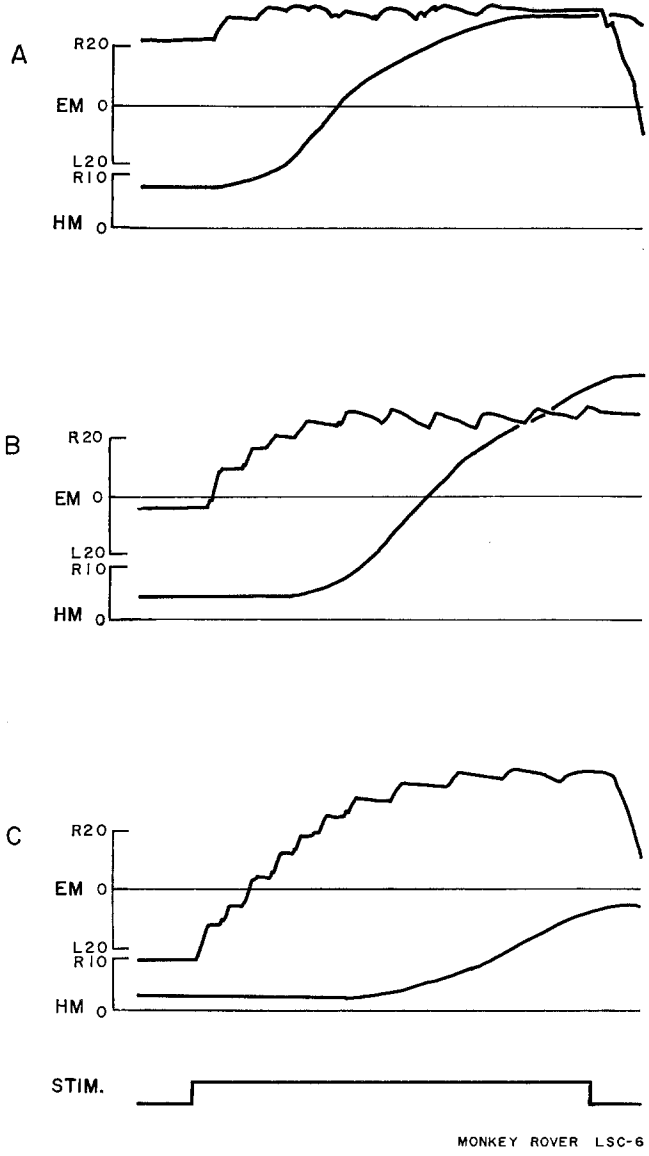


Fig. 3. Horizontal eye movement (EM) and head movement (HM) in response to a 2 sec stimulus train ($15 \mu\text{A}$ 0.5 msec pulses at 300/sec) delivered to the left superior colliculus. In (A) the eye starts from the right of center; in (B) the eye starts approximately centered in the orbit; and in (C) the eye starts from the left of center. Note the different scales (in degrees) for head and eye position. Right is up for both head and eye

saccades after the first one became smaller. These effects on the eye movements were paralleled in the head movements: the probability of the head movement increased with increasing current, and its latency decreased. Head movement

The lack of a sharp electrical threshold and the variability of evoked head movements suggest that there is no simple relation between activation of neurons in a particular region of the colliculus and head movements. The dependence of the elicited head movement on initial eye position further suggests that the colliculus does not code head movements in the monkey because discharge properties of collicular neurons do not depend on eye position (Schiller and Koerner, 1971; Schiller and Stryker, 1972; Wurtz and Goldberg, 1972).

These results are in agreement with a recent study by D. L. Robinson and C. D. Jarvis (1974). They report that the discharge of intermediate-layer colliculus cells in the monkey is related in timing and magnitude to the intended eye movement rather than to head movement; collicular cells related to head movement or position were not found. Thus, the stimulation and recording data for the monkey are complementary, suggesting that the superior colliculus is not the prime site for the initiation of head movements or the elaboration of head-eye coordination.

It would seem then that the head movements evoked by electrical stimulation are elaborated at some site other than the colliculus. Because the likelihood and latency of an evoked head movement depends on eye position in the orbit, such an elaboration must be carried out by some structure which receives information about eye position. Since all head movements we observed following collicular stimulation were of long latency (> 90 msec with eye movement at 25 msec), they could be accounted for by a model in which the head movement controller receives *only* eye position information. This eye position information might be either afferent or corollary to the oculomotor outflow. Thus, in the case of collicular stimulation, it appears that eye position information could serve as the sole link between head and eye systems, so that when the eyes are moved to extreme positions, they begin to drag the head along behind them, so to speak.

Recent work by Bizzi and collaborators (1972) has shown, however, that during natural head-eye movements toward visual targets the head follows the eyes with very short latency and activation of the neck muscles actually *precedes* activation of the eye muscles. To account for the rapidity and appropriateness of these head movements, they propose that the head movement controller receives both a visual error signal and information about eye position in orbit. Our data suggest that electrical stimulation of the superior colliculus, which produces a potent eye movement signal, does not serve to produce an adequate visual error signal for the head movement controller. If such a signal is produced at all, it must occur only after a delay so long that the eye position signal alone would be sufficient to move the head.

The question may be raised whether or not the concept of collicular function described here for the monkey can apply to other species. In species whose ocular motility is extremely restricted, such as the owl which exhibits a maximum of 1.5° of eye movement (Steinbach and Money, 1973), the output of the superior colliculus might well code head movements directly since a target at a given retinal eccentricity requires a unique head movement for fixation. Animals with somewhat more extensive eye movements, such as the cat which can move its eyes about 20° to either side of the midline (Stryker and Blakemore, 1972), could code head movements accurately in the colliculus only if they were to employ a strategy of moving the head to re-center the eyes in orbit after each new fixation. One may

predict, then, that animals using such a scheme will show extreme reluctance to maintain eccentric fixation and will also have a closer association between eye and head movements. It is only among animals that are willing to maintain an eccentric position of the eyes in orbit such as the monkey (Bizzi *et al.*, 1972) that difficulties arise from the coding of head movements in the colliculus.

Data on the tecto-spinal pathways in several species appear to be in harmony with the role of the superior colliculus in head movement as presented here. Although there are direct projections from superior colliculus to the cervical spinal cord (Altman and Carpenter, 1961; Nyberg-Hansen, 1964; Myers, 1963), a recent review of the anatomical evidence on descending pathways from the tectum in tree shrew and other species suggests that the *major* influence of the superior colliculus on the spinal cord involves at least one relay in the brainstem (Harting, Hall, Diamond and Martin, 1973). This observation is consistent with the findings of Anderson, Yoshida and Wilson (1971) who have analyzed postsynaptic potentials in neck motoneurons following collicular stimulation in the cat. They show that in the contralateral motoneurons EPSP's are produced by the colliculus mainly through activation of reticulo-spinal neurons, and are at least disinaptic. Such a relay in the brainstem could be the site at which eye-position information, either corollary or afferent, is fed into the head-movement control system.

Acknowledgements. We thank Mss. Susan Volman and Cynthia Richmond for their technical assistance and Ms. Kathy Anderson for her secretarial help. We are grateful to Profs. Hans-Lukas Teuber and Emilio Bizzi for critical readings of the manuscript.

This study was supported by a research grant from the National Eye Institute (EY00756) and a predoctoral training grant from the National Institute of General Medical Sciences (GM01064).

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