

## Response properties of eye movement-related neurons in the monkey superior colliculus

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The superior colliculus may be part of a system which acquires visual targets for foveal viewing<sup>8</sup>. This foveation hypothesis states that the superior colliculus is involved in coding the location of an object relative to the fovea and in eliciting saccadic movements which produce foveal acquisition of the object. Evidence offered in support of this view is derived from electrical stimulation and single unit recording experiments.

In alert monkeys, the amplitude and direction of saccadic eye movements produced by electrical stimulation are a function of the site of stimulation within the superior colliculus rather than the parameters of stimulation<sup>4,6,8</sup>. Saccades have up-components if elicited by stimulation of medial regions of the superior colliculus and have down-components if elicited by stimulation of lateral regions. Elicited movements are small rostrally and large caudally.

The maximal discharge of neurons in the deeper layers of the superior colliculus occurs prior to an eye movement with a particular direction and amplitude<sup>5-7,9</sup>. However, each neuron has a movement field, *i.e.*, the neuron discharges prior to a range of movements of similar directions and amplitudes. The finding that the movement fields of superior colliculus neurons are relatively large (up to 20° in diameter) has been used to argue against the foveation hypothesis<sup>9</sup>. If, however, the response of superior colliculus neurons is sharply tuned to particular movements, this argument may not be so compelling. The major purpose of this experiment was to describe, in more detail, the movement field properties of neurons in the deeper layers of the superior colliculus. A secondary purpose was to explore, further, the topographical organization of the movement fields.

Two monkeys (*Macaca mulatta*) were trained to track a visual target presented on a Hewlett-Packard 1310A oscilloscope with a CRT viewing area of ~~4.4~~ 6 cm × 6 cm. The horizontal and vertical position of the target, a dot subtending a visual angle of less than 0.1°, was controlled by a PDP-8/I computer and two 12 bit digital-to-analog converters. The oscilloscope was placed ~~5.6~~ 35 cm in front of the subject. At this distance the maximum horizontal excursion of the target was ± 25°; the maximum vertical excursion, ± 20°. Horizontal and vertical eye movements were measured

27 X 37

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using a magnetic field, search coil technique<sup>2</sup>. Visual input was restricted to the eye from which eye movement records were obtained by placing an opaque eye patch over the other eye.

During recording sessions, animals were seated in a chair with head restrained<sup>1</sup>. A movable microelectrode positioner and teflon-coated tungsten microelectrodes were used to record, extracellularly, the activity of neurons in the superior colliculus. Lesions were placed at the maximum depth of tracks in which responsive units were encountered and, at the termination of the experiment, 50  $\mu\text{m}$  frozen sections were mounted and stained with thionin. Reconstructions of the electrode paths were made based upon lesion sites and measurements of electrode position taken during recording sessions.

When a neuron was sufficiently isolated from background noise, the response of the neuron to spontaneous eye movements and to a standard tracking task was determined. The standard tracking task consisted of 24 trials. Each trial started when the target appeared in the center of the screen. The animal was required to fixate the target for 2 sec and the target was then moved instantaneously to one of the 24

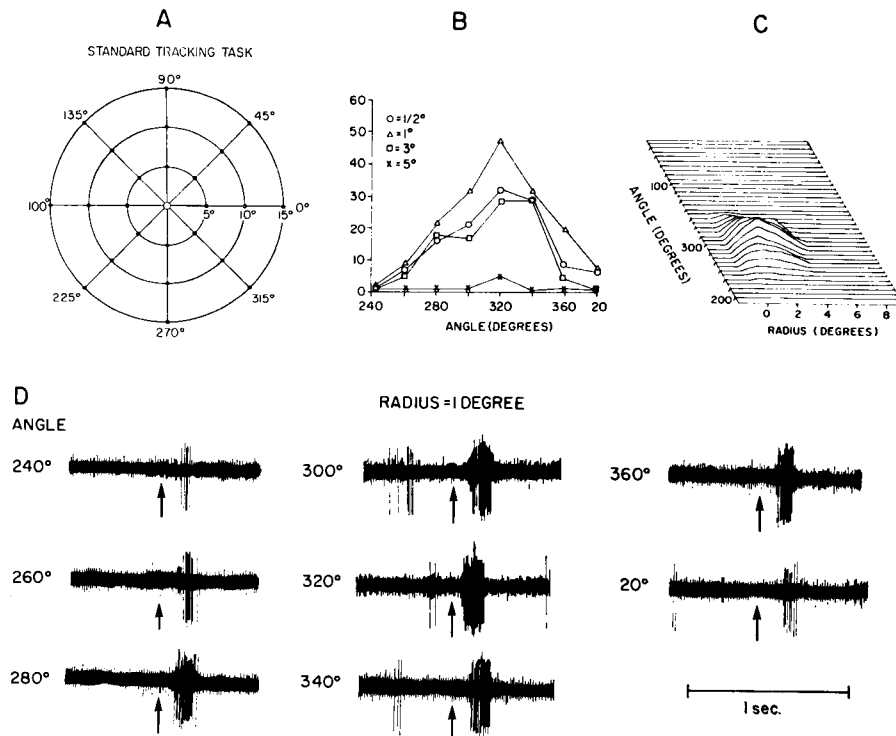


Fig. 1. A: the standard tracking task. If subject fixated the center dot for 2 sec, the target was moved to one of the 24 positions indicated by the filled circles. B: burst-index (see text) as a function of angle of movement. Each point represents the median value of three observations. C: burst-index as a function of angle and radius of eye movement. D: response of a superior colliculus unit to a series of saccades with a 1° radius and varying in direction. The onset of target movement is indicated by the arrow below each trace.

positions shown in Fig. 1A. If the animal acquired the new target position within 500 msec and maintained fixation for an additional 2 sec, a liquid reinforcement was given. Horizontal and vertical eye position signals were sampled each 10 msec and compared with target position. The horizontal origin, vertical origin, and angle and radius of each target movement were controlled by the experimenter via on-line interaction with the computer. Additionally, the experimenter received a display of spike frequency at the end of each trial. If unit activity was related to spontaneous or tracking eye movements, the movement field of the unit was plotted by having the monkey make saccades to many different positions in the visual field. To ensure that movement-related discharges were not the result of retinal image displacement, the activity of each unit was also observed during spontaneous eye movements occurring in total darkness.

Spike activity, vertical and horizontal eye movements, and target position were recorded on magnetic tape. Programs were written for the PDP-8/I computer to aid in describing the relation between spike frequency and changes in eye position. Results obtained from these programs and reproductions of unit activity, horizontal and vertical eye position, and target position obtained with a mirror galvanometer recorder were used to plot the responsiveness of each unit.

Detailed maps of the movement fields of 18 neurons in the intermediate and deeper layers of the superior colliculus were obtained. The movement fields of 7 additional units were studied in less detail. In general, our results confirm the findings of previous investigators<sup>6-9</sup>. Unit discharge occurs prior to saccadic movements, is specific to the direction and amplitude of contralateral saccades, and is independent of the initial position of the eye in the orbit. Many of these units also respond to visual stimuli.

The response of a neuron located in the anterior tip of the superior colliculus is illustrated in Fig. 1. Fig. 1B plots burst-index (the difference between the number of spikes occurring during a 500 msec period of center target fixation and the number of spikes occurring in the 500 msec following the movement of the target to a new location) as a function of the angle of eye movement. The data for 4 different movement amplitudes (0.5, 1, 3, and 5°) are shown. A three-dimensional plot of the same data is shown in Fig. 1C. The maximal discharge of this neuron occurred prior to small right saccades with a downward component (1° in amplitude at an angle of 320°). Movements within the movement field but less than or greater than 1° in amplitude were preceded by a less vigorous response. Similarly, if the angle of movement deviated from 320°, less vigorous responses were observed. A series of single trial recording at the optimal amplitude of movement, 1°, is shown in Fig. 1D.

Fig. 2 plots the response of 4 neurons which displayed maximal discharges prior to eye movements of 1, 3, 7 and 10° in amplitude. The optimal direction for the discharge of each of these neurons was 80, 20, 160, and 140°, respectively. As previously reported<sup>7</sup>, the size of the movement field increases as a function of the amplitude of the optimal movement. The response of a neuron located in the anterior superior colliculus is illustrated in Fig. 2A. The discharge of this unit preceded movements of less than 0.5° in amplitude and movements as large as 2° in amplitude, a range of

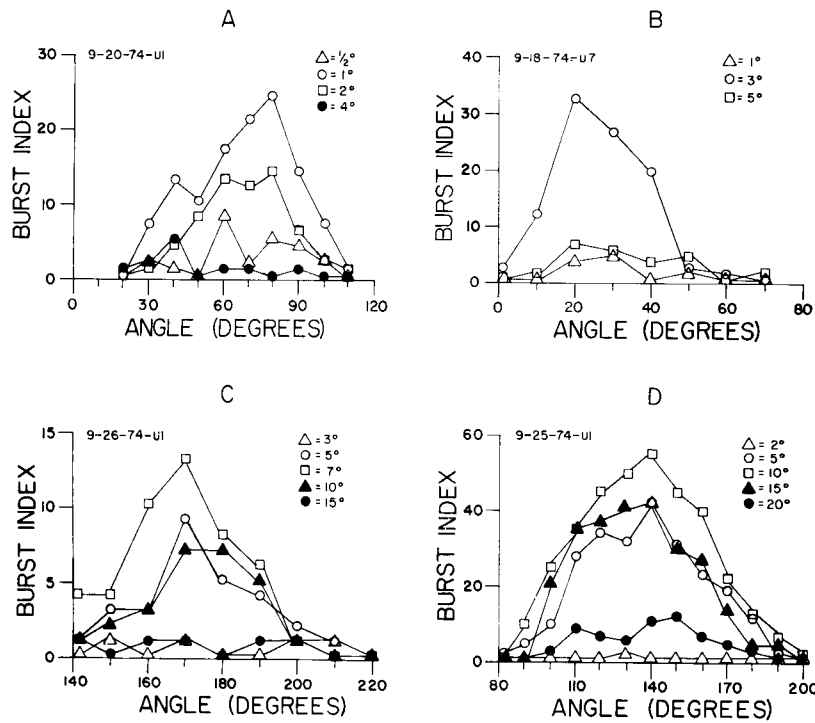


Fig. 2. Burst-index as a function of angle of eye movement for 4 superior colliculus neurons. Note that the scale is different for each plot.

approximately  $2^\circ$ . In contrast, the response of a unit located more caudally is shown in Fig. 2D. A discharge of this unit preceded movements with amplitudes varying from less than  $5^\circ$  to  $20^\circ$ , a range of  $15^\circ$ . Units with even larger movement fields were encountered but we were unable to plot these fields in detail since saccades greater than  $20^\circ$  were rarely observed during visual tracking. If the target was displaced  $25^\circ$ , the target was acquired with two saccades, one of approximately  $20^\circ$  and a second of approximately  $5^\circ$ .

The unit illustrated in Fig. 2D discharged prior to or during movements ranging in direction from  $85$  to  $90^\circ$  and in amplitude from less than  $5$  to  $20^\circ$ . Response magnitude was reduced by  $50\%$  at angles of  $120$  and  $170^\circ$  and was reduced by  $80\%$  or greater at amplitudes of  $2$  or  $20^\circ$ . Much sharper tuning of movement fields was seen in the anterior superior colliculus. Fig. 2B illustrates the response of a unit which gave a vigorous discharge prior to up and right movements of  $3^\circ$  amplitude but did not reliably discharge prior to  $1^\circ$  or  $5^\circ$  movements in the same direction. All the units we have encountered in the intermediate and deeper layers of the superior colliculus show response tuning similar to the neurons illustrated in Fig. 2.

As Fig. 3 illustrates, we have observed systematic changes in the size and location of movement fields as a function of recording site in the superior colliculus. As successive neurons are encountered along a single electrode penetration, two charac-

teristics of the eye movements producing maximal discharge rates show a systematic change. There is an increase in the amplitude of the optimal eye movements accompanied by an increase in the downward component of the optimal direction of movement (Fig. 3B). A similar change in receptive field size and location as a function of recording site has been observed in the upper layers of the superior colliculus<sup>3</sup>. These findings appear to disagree with stimulation experiments in which the amplitude and direction of elicited saccades remain relatively constant as a function of depth in the superior colliculus. This apparent discrepancy is most likely due to the fact that our electrode penetrations were in the vertical stereotaxic plane and the electrode

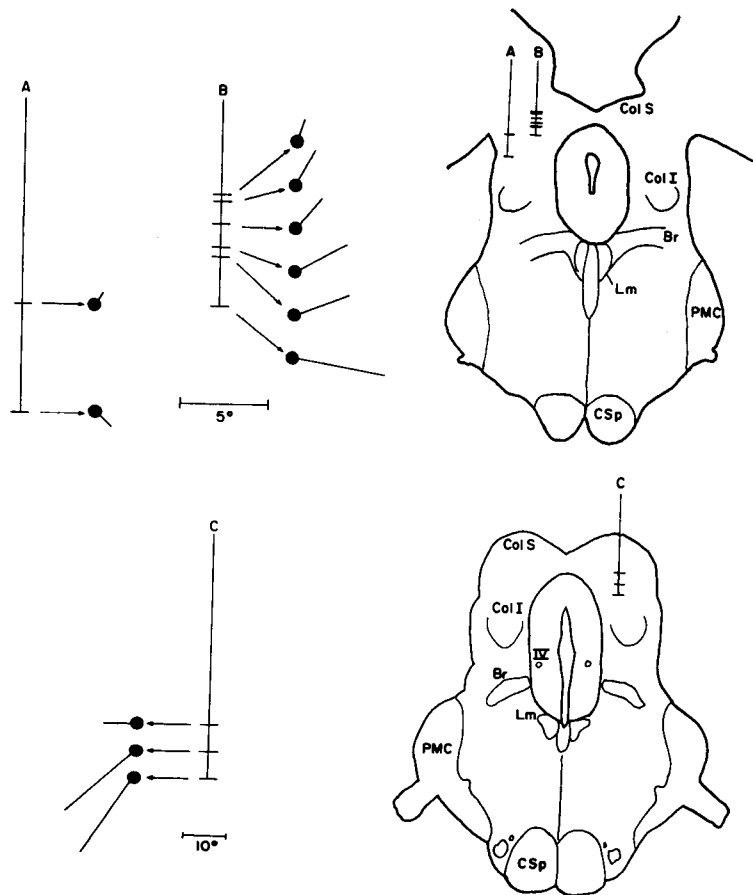


Fig. 3. Representative sections of the superior colliculus showing recording sites and the direction and length of saccades which were preceded by the maximal discharge of the unit. Three penetrations into the superior colliculus are labeled A, B and C. Horizontal marks indicate the positions of eye movement-related neurons encountered along the reconstructed electrode paths. Enlargements of the electrode paths are shown adjacent to the brain stem sections. The length of the line originating from the filled circle is proportional to saccade amplitude and the angle of tilt indicates the optimal direction of movement. Br, brachium conjunctivum; Col I, inferior colliculus; Col S, superior colliculus; CSp, corticospinal tract; IV, trochlear nerve; Lm, medial longitudinal fasciculus; PMC, middle cerebellar peduncle.

moved caudally in the superior colliculus as depth increased. In Robinson's experiment<sup>4</sup>, electrodes were oriented at an angle of 45° with respect to the vertical stereotaxic plane and were approximately perpendicular to the orientation of the superior colliculus.

In summary, our data do not provide unequivocal support for the foveation hypothesis<sup>8</sup> of superior colliculus function. Movement fields in the rostral superior colliculus are small and sharply tuned. Caudally, movement fields are much larger and although the neuronal response is markedly reduced at the periphery of movement fields, tuning is relatively broad. It is possible, of course, that the neurons in the deeper layers of the superior colliculus provide inputs into a subsequent stage of the oculomotor system where efferent signals with greater resolution are generated. Certainly, the responses of superior colliculus neurons precede the onset of eye movements sufficiently to permit subsequent signal extraction.

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