

The functional organization of the primate superior colliculus: A motor perspective

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Introduction

The deeper layers of the superior colliculus (SC) are a site where visual, auditory and somatosensory signals converge and an area that contains neurons with motor properties (see Sparks and Mays, 1983; Schiller, 1984; Stein, 1984, for recent reviews). Based upon this observation, many investigators have suggested that the SC may be a brain region where signals from various sensory modalities are translated into common motor commands — commands for orienting the eyes, head and pinnae toward the source of significant or novel environmental stimuli. This chapter summarizes what is known about the motor signals found in the SC and, based upon this information, discusses the transformations of sensory signals that are required for a sensory/motor interface.

Results

Although electrical stimulation studies suggest that the SC may contain neurons related to movements of the eye, head, and external ears (Schaefer and Schneider, 1968; Syka and Radil-Weiss, 1971; Robinson, 1972; Schiller and Stryker, 1972; Harris, 1980; Roucoux et al., 1980; Stein and Clamann, 1981; McHaffie and Stein, 1982), only the signals involved in initiating saccadic eye movements have been studied in detail (Schiller and Koerner, 1971; Wurtz and Goldberg, 1972; Sparks et al., 1976).

One type of neuron found in the intermediate layers of the SC generates a high-frequency burst of spike activity that begins 18–20 mseconds before saccade onset (see Fig. 1). The activity of these neurons is tightly coupled to saccade onset, and in behavioral situations in which a visual target sometimes elicits a saccade and sometimes fails to do so, the probability of the high-frequency spike burst is almost perfectly correlated with the probability of saccade occurrence (Sparks, 1978). Collicular neurons discharge prior to saccades of a particular direction and amplitude, regardless of initial eye position (Schiller and Koerner, 1971; Wurtz and Goldberg, 1972; Sparks et al., 1976). Thus, their discharge is not related to moving the eye to a particular position in the orbit but to motor error, the change in eye position required to direct gaze to the target location. As illustrated in Fig. 1, each of these neurons has a movement field — i.e., each neuron discharges before a range of saccades that have particular directions and amplitudes (Wurtz and Goldberg, 1972; Sparks et al., 1976).

Neurons with motor properties are arranged topographically within the SC. In the monkey, this motor map has been described in detail using microstimulation methods (Robinson, 1972) and chronic single unit recording experiments have confirmed the basic features of the motor map (Schiller and Stryker, 1972; Wurtz and Goldberg, 1972; Sparks et al., 1976). Since each neuron fires before a range of saccades, it follows that a large popula-

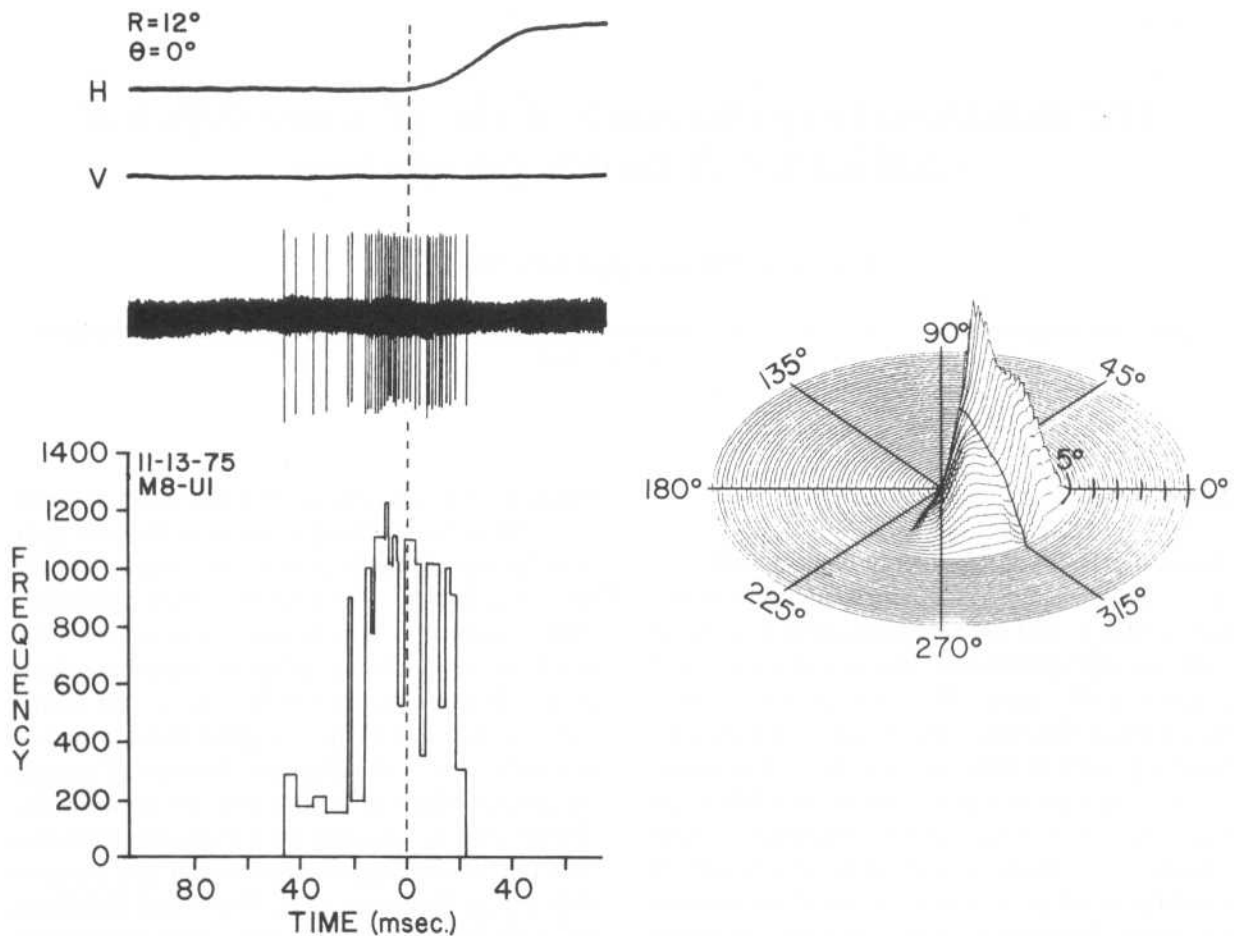


Fig. 1. Left. Discharge pattern recorded from a typical saccade-related burst neuron in the superior colliculus. H, Horizontal eye position; V, vertical eye position. Middle tracing: spike discharge. Bottom graph: instantaneous spike frequency as a function of time. The dotted line represents the onset of the eye movement. Right. Three-dimensional representation of the number of spikes as a function of the angle and amplitude of eye movements. The maximal burst (48 spikes) preceded 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° , fewer spikes were observed. Adapted from Sparks et al. (1976).

tion of collicular neurons will discharge before a particular saccade (McIlwain, 1975; Sparks et al., 1976). The population response is characterized by a temporal and spatial gradient of activity (Sparks and Mays, 1980). Neurons in the center of the population fire earlier and more vigorously than surrounding cells. Neurons on the fringe of the active population fire weakly and their activity may follow, rather than precede, saccade onset.

Although the vigor of discharge of a particular saccade-related burst cell varies for different movements within the movement field, information concerning saccade direction and amplitude is not contained within the discharge of a single cell (Sparks and Mays, 1980). As illustrated in Fig. 2, except for the maximal discharge which precedes saccades to the center of the movement field, the discharge of SC neurons is ambiguous with respect to saccade

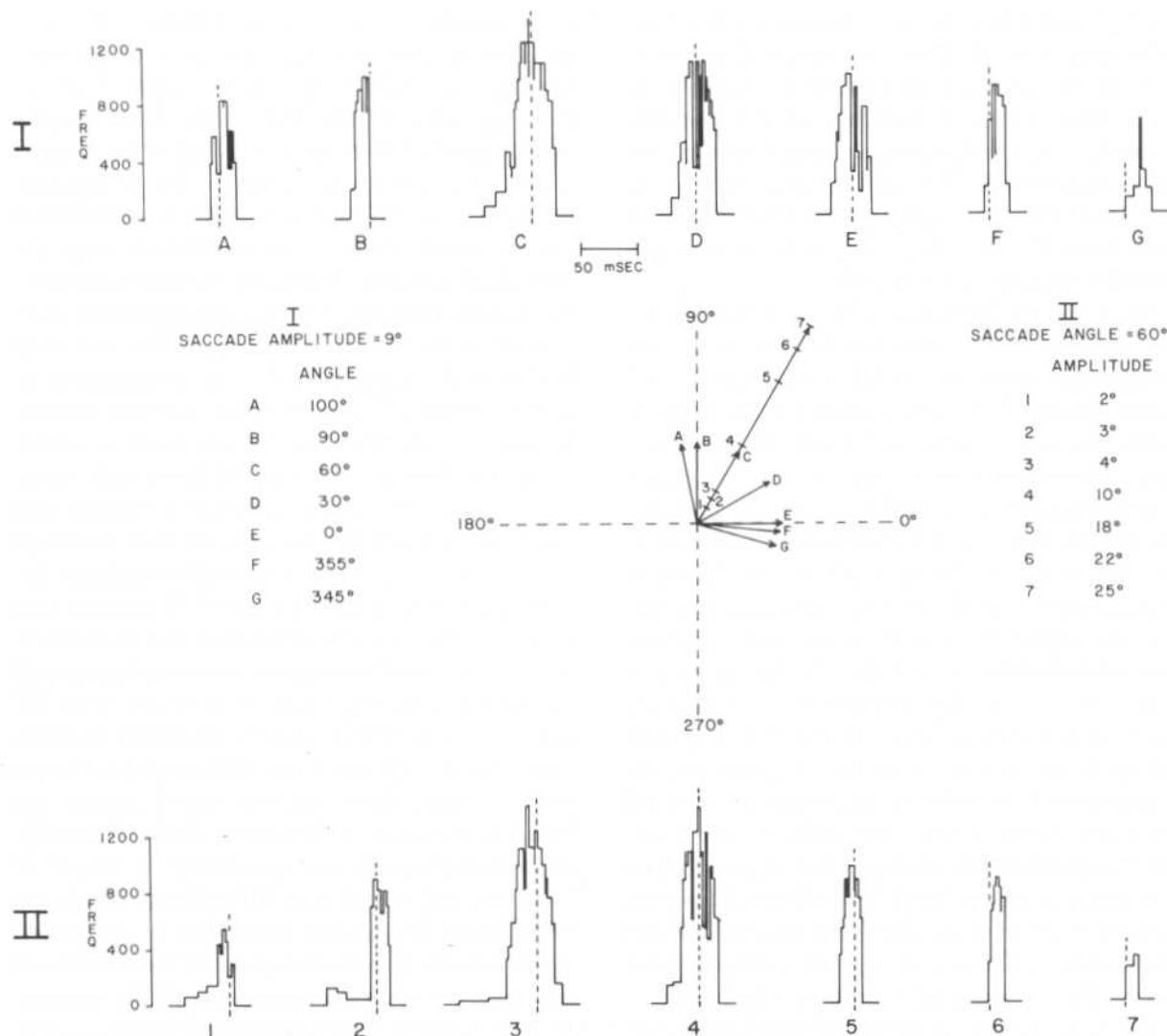


Fig. 2. Variations in the configuration and timing of the discharge of a typical saccade-related burst neuron. I. Instantaneous spike frequency records for seven saccades of the optimal amplitude (9°) but differing in direction. The dotted line represents saccade onset. II. Instantaneous spike frequency records for seven saccades of the optimal direction ($\theta = 60^\circ$) but differing in amplitude. Note that for saccades on the fringe of the movement field, the neural discharge may follow, rather than precede saccade onset. Note, too, the similarity of the burst profile in B, F, 2 and 6, although these bursts preceded saccades with large differences in direction and amplitude. From Sparks and Mays (1980).

direction or amplitude. Identical discharges may precede many saccades having different directions and amplitudes (Sparks and Mays, 1980). Also, the discharge of different saccade-related burst units, some which discharge maximally to small saccades and some which discharge maximally to large sac-

cades, is indistinguishable (Sparks and Mays, 1980). Thus, unlike the primary vestibular afferents, for example, which encode head velocity by firing rate, the SC does not generate specific rates of firing for different amounts of motor error.

In summary, two major conclusions can be

reached concerning the saccade-related motor signals found in the SC. First, the activity of collicular neurons encodes the desired change in eye position, not a movement to a particular orbital position. Secondly, saccade direction and amplitude are encoded anatomically. It is the location of the active neurons within the topographical map of movement fields, not their frequency of firing, that specifies the trajectory of a saccade.

What are the implications of these findings for the sensory/motor transformations that are thought to occur within the SC? First, since the collicular command specifies a change in eye position rather than a movement that directs gaze to a particular spatial location, sensory systems must provide a signal of the desired change in eye position, not just the location of a stimulus in head, body or retinal coordinates. Secondly, since it is the site of activity within the SC that encodes saccade direction and amplitude, sensory signals must be translated into a format compatible with this anatomical code — i.e., a particular subset of collicular neurons must be activated in order to produce a specific change in eye position. Consider, for example, the translation of an auditory signal into a command for a saccadic movement. The auditory system uses interaural differences in time, intensity and phase to localize targets in “head” coordinates. However, in order to compute the difference between the current direction of gaze and target position, the position of the eye in the orbit must also be known.

We have recently completed experiments conducted to test these hypotheses (Jay and Sparks, 1984). Monkeys were trained to look to both visual and auditory targets in a completely darkened room. A hoop, 6 feet in diameter, surrounded the monkey seated inside magnetic fields used to measure eye position. Rotation of the hoop by a computer-controlled stepping motor changed the elevation of the miniature speaker attached to the hoop. Another stepping motor controlled the azimuth of the target by moving the speaker around the hoop. A small light-emitting diode (LED) mounted at the center of the speaker permitted the presentation of visual or auditory stimuli. Also, three additional

LEDs were used to control initial fixation. The center LED was placed directly in front of the monkey; the others were 24° to the left and right of center. On a typical trial, one of the three fixation lights was illuminated. If the animal looked to the fixation target and maintained fixation for a variable period, an eccentric stimulus (light or noise burst) was presented while the center fixation target remained illuminated. Reward was contingent upon maintaining fixation of the center target until, after a variable interval, it was extinguished, and then looking to the location of the eccentric auditory or visual stimulus. This delayed saccade task permitted unit activity linked to stimulus onset to be distinguished from activity coupled to saccade onset.

The goal of the experiment was to answer two basic questions. First, do neurons that discharge before saccades to visual targets also discharge before saccades to auditory targets? If they do, this indicates that auditory and visual signals have already been converted into the same coordinates and are sharing a motor circuit. If, however, some SC neurons burst before visually triggered saccades and other SC neurons burst before saccades to auditory targets, then separate motor circuits are being used, at least at the level of the SC. Secondly, are auditory signals reaching the SC in “head” or “motor error” coordinates? If auditory signals are organized in head coordinates, then in our experiments (in which the head was fixed) the response of acoustically responsive neurons should be independent of initial fixation position and depend entirely upon the azimuth and elevation of the speaker. However, if auditory signals have been translated into motor error coordinates, then the neural response to acoustic stimuli should depend upon both the position of the speaker in space and the position of the eyes in the orbit.

We found (Jay and Sparks, 1984) that SC neurons that burst prior to saccades to visual targets also burst before saccades to auditory targets. This indicates that, at or before reaching the level of the SC, auditory and visual signals have converged onto a common motor pathway for the generation of saccadic movements.

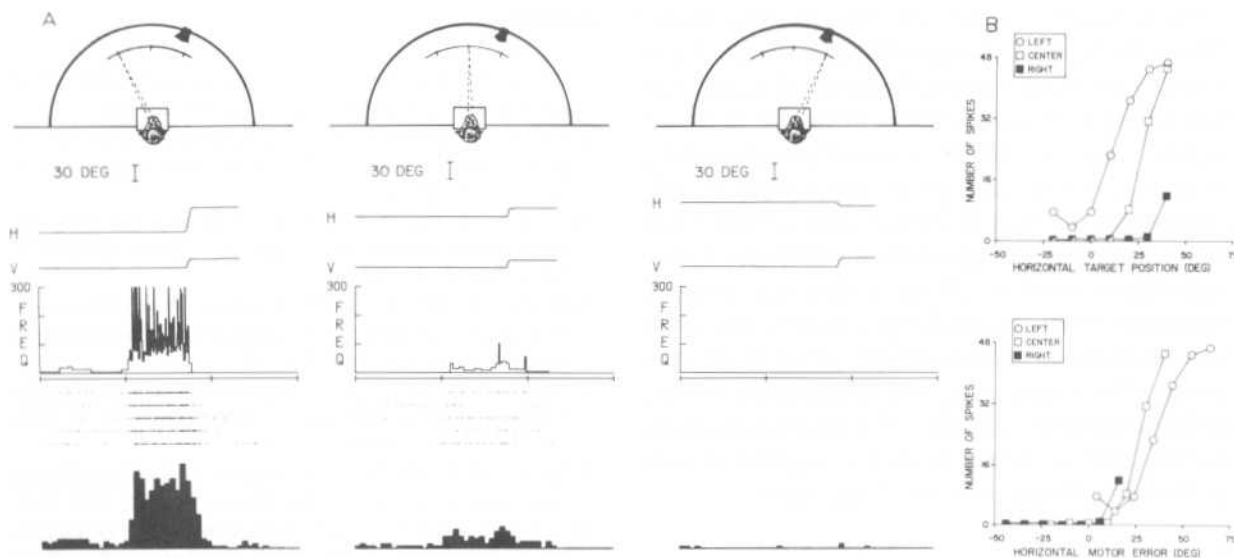


Fig. 3. The effects of eye position on the response of a single SC cell to an auditory stimulus. A. The speaker was placed 20° to the right and elevated 6° while the fixation position was varied between 24° left (left), center (center) and 24° right (right). The time base represents 3 seconds; target onset occurred at 1 second. Horizontal (up = right) and vertical (up = up) eye position traces are shown in the top row. Instantaneous firing rates are shown for single trials in the second row. Next, rasters displaying unit activity for five trials are illustrated. A cumulative histogram for these trials is displayed on the bottom row. B. A plot illustrating the shift in the position of the receptive field (top) when eye position was varied. The same data are aligned when plotted in motor error coordinates. From Jay and Sparks (1984).

The effects of varying eye position upon the response to auditory stimulation were tested in 121 cells, all but two of which were responsive to visual and auditory stimulation. Statistically significant ($P < 0.05$) effects were obtained in 99 of the 121 SC cells tested. Typical data are illustrated in Fig. 3. For the trials shown, the speaker was positioned 20° to the right and 6° above the primary eye position. Presentation of the noise burst evoked a vigorous neural discharge when the monkey was looking at the left fixation target. When the monkey was viewing the center or right fixation lights, an identical noise burst presented in the same spatial location resulted in a response that was markedly attenuated or completely absent. The average number of spikes evoked by the noise burst is plotted as a function of the horizontal position of the speaker for the three different fixation positions in Fig. 1b (top). The receptive field of the neuron shifted with the position of the eyes in the orbit. Below, the av-

erage number of spikes is plotted as a function of horizontal motor error, the horizontal component of the movement required to look to the auditory targets. The data obtained while the monkey viewed the three fixation lights are closely aligned in this plot. Thus, the discharge of this neuron depended upon the movement required to look to the target, a factor that is a function of the position of the eyes in the orbit as well as the position of the target.

These findings suggest that a representation of motor error is formed by subtracting eye position from a head-centered representation of target location. Consequently, the map of auditory space found in the monkey SC is not static. With each movement of the eyes in the orbit, the population of neurons responsive to a stationary auditory stimulus changes to a new location within the SC — a location that represents the new motor error signal.

These results complement earlier experiments (Mays and Sparks, 1980; Sparks and Porter, 1983) in which we found that the discharge of visual neurons in the intermediate layers of the SC does not depend upon stimulation of a specific region of the retina. Using trials in which an intervening saccade changed the position of the eyes after a brief visual target had been extinguished, we discovered neurons (quasi-visual or QV cells) that were visually responsive but with discharge patterns that were best described as encoding motor error. If the eyes moved after a brief target had disappeared, the site of QV cell activity shifted to a location representing the trajectory of the eye movement required to look to the remembered position of the target.

Conclusions

In summary, results of several recent experiments can best be explained by assuming that the SC is organized in motor coordinates. Motor error is encoded anatomically; it is the site of activity within the colliculus, not discharge frequency, that specifies saccade direction and amplitude. This command format imposes constraints upon the configuration of signals that can initiate saccades and determines the required transformations of sensory signals. Inputs to the colliculus must specify (by activating a particular subset of collicular neurons) the desired change in eye position, not merely the location of the target in head, body or retinal coordinates. This requires dynamic maps of auditory and visual space. With each change in eye position, the site of acoustically and visually induced activity shifts to a location that specifies the eye movement required to direct gaze to the target location. In this manner, auditory and visual signals are translated into common motor error coordinates, are maintained in register with the static motor map, and converge onto a shared motor pathway for the generation of saccadic eye movements.

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