JOURNAL OF NEUROPHYSIOLOGY
Vol. 57, No. 1, January 1987. *Printed in U.S.A.*

Sensorimotor Integration in the Primate Superior Colliculus. I. Motor Convergence

MARTHA F. JAY AND DAVID L. SPARKS

Department of Physiology and Biophysics and the Neurosciences Program, University of Alabama, Birmingham, Alabama 35294

SUMMARY AND CONCLUSIONS

1. Orienting movements of the eyes and head are made to both auditory and visual stimuli even though in the primary sensory pathways the locations of auditory and visual stimuli are encoded in different coordinates. This study was designed to differentiate between two possible mechanisms for sensory-to-motor transformation. Auditory and visual signals could be translated into common coordinates in order to share a single motor pathway or they could maintain anatomically separate sensory and motor routes for the initiation and guidance of orienting eye movements.

2. The primary purpose of the study was to determine whether neurons in the superior colliculus (SC) that discharge before saccades to visual targets also discharge before saccades directed toward auditory targets. If they do, this would indicate that auditory and visual signals, originally encoded in different coordinates, have been converted into a single coordinate system and are sharing a motor circuit.

3. Trained monkeys made saccadic eye movements to auditory or visual targets while the activity of visual-motor (V-M) cells and saccade-related burst (SRB) cells was monitored. The pattern of spike activity observed during trials in which saccades were made to visual targets was compared with that observed when comparable saccades were made to auditory targets.

4. For most (57 of 59) V-M cells, sensory responses were observed only on visual trials. Auditory stimuli originating from the same region of space did not activate these cells.

5. Yet, of the 72 V-M and SRB cells studied, 79% showed motor bursts prior to saccades to either auditory or visual targets. This finding indicates that visual and auditory signals, originally encoded in retinal and head-centered coordinates, respectively, have undergone a transformation that allows them to share a common efferent pathway for the generation of saccadic eye movements.

6. Saccades to auditory targets usually have lower velocities than saccades of the same amplitude and direction made to acquire visual targets. Since fewer collicular cells are active prior to saccades to auditory targets, one determinant of saccadic velocity may be the number of collicular neurons discharging before a particular saccade.

INTRODUCTION

Movements that orient the eyes and head toward the source of auditory, somatosensory, or visual stimuli are based on complex transformations of sensory signals into motor commands. Necessary neural computations include the generation of signals representing the location of the target in space and those specifying the metrics of the movement needed to direct gaze to the target. Moreover, signals of target location must be computed differently for each sensory system. Information about the location of a visual target is based on the site of retinal activation, the position of the eyes in the orbit as well as the current orientation of the head and body. The spatial location of a cutaneous stimulus must be determined using information about the position of the stimulus on the body surface and the angles of intervening joints. Auditory targets

are localized in head coordinates based on interaural differences in the intensity and timing of acoustic stimuli.

These sensory signals, originally encoded in retinal, body, or head coordinates, could be translated into motor coordinates in a number of ways. The signals indicating the presence of a saccade target could remain in the distinct coordinate system of that sensory modality and not be transformed into motor coordinates until the various pathways converge onto a final common pathway. Alternatively, the different sensory signals could first be translated into the same coordinates and then converge onto a single premotor pathway for the generation of saccades.

The deeper layers of the superior colliculus (SC) contain neurons responsive to auditory, visual, and somatosensory stimuli (22, 23) as well as neurons involved in the initiation of saccadic eye movements (15, 20, 24). The purpose of the first paper in this series was to determine whether saccades to auditory and visual targets are generated by a shared premotor pathway in the SC. The second paper investigates the coordinate systems employed by auditory and visual neurons in the SC for encoding the spatial location of saccade targets.

We recorded the activity of collicular neurons while monkeys were generating saccades to auditory and visual targets. The activity of two types of cells, previously identified in the primate SC, was of particular interest. Cells of each type are found in the intermediate layers and generate presaccadic activity tightly coupled to the onset of saccades within their movement field (the range of saccade directions and amplitudes preceded by an increase in activity). Visual-motor (V-M) cells have sensory receptive fields and movement fields (20, 24). They produce a burst of activity 40–60 ms after a stimulus is presented in their visual receptive field and a second increase in activity beginning up to 100 ms before saccades to acquire the target (15, 20, 24). It is not known, however, if the sensory and motor components of their response are restricted to visual stimulation or whether they would also be evoked by auditory or somatosensory stimuli. Saccade-related burst (SRB) cells generate a discrete high-frequency burst of activity beginning ~20 ms before visually triggered saccades to the center of their movement fields (21). Although SRB neurons are known to be active prior to spontaneous saccades (20, 24) and perhaps before the quick phases of caloric and optokinetic nystagmus (16), it is not known if they participate in the initiation of saccades to auditory targets.

In the present study, monkeys were required to generate saccades of comparable directions and amplitudes to acquire auditory or visual targets while the activity of collicular neurons was monitored. The major purpose of the study was to test the hypothesis that neurons discharging before saccades to visual targets also discharge before saccades to auditory targets. If they do, this would indicate that auditory and visual signals, originally encoded in different coordinates, have already been converted into the same coordinates and are sharing a motor circuit. If, however, some collicular neurons burst before saccades to auditory targets and a different population of neurons burst before visually triggered saccades, then separate motor circuits are being used at the level of the SC.

The velocity of saccades to auditory targets or spontaneous saccades is usually lower than the velocity of saccades to visual targets (25, 26). The SC could be involved in regulating saccadic velocity since lesions of the SC (18) and microinjections of a GABA agonist (muscimol) into the SC reduce saccadic velocity (3). Thus a secondary objective of the experiment was to examine the relationship between the velocity of saccades to auditory and visual targets and measures of presaccadic spike activity.

Brief reports of these findings have appeared elsewhere (4, 5).

METHODS

Experimental subjects and surgical procedures

Two adult rhesus monkeys (*Macaca mulatta*) served as subjects and, under barbiturate anesthesia (pentobarbital sodium), underwent three sterile surgical procedures. First, stainless steel bolts were implanted into the skull and attached to a lightweight aluminum crown used to stabilize the head during training and recording sessions. In the second procedure, a preformed coil consisting of three turns of insulated, multistranded stainless steel wire was sutured to the sclera (7). The implanted coil was used to measure horizontal and vertical eye position with a sensitivity of at least 0.25° (1). After behavioral training, a ring-mount stainless steel cylinder

was positioned stereotaxically over the SC (stereotaxic coordinates: anterior-posterior 0.0 mm; medial-lateral 0.0 mm).

Recording procedures and visual/auditory stimulation

Extracellular unit activity was monitored using Parylene-coated tungsten microelectrodes inserted through the dura in a 21-gauge stainless steel cannula. Signals were filtered above 3,000 Hz to reduce contamination by the 26-kHz magnetic fields. Conventional recording devices were used to amplify, monitor, and discriminate single cell activity. Electrode position in the colliculus was routinely checked by stimulating through the recording electrode. As the electrode was lowered, the abrupt transition of threshold current from 200 μA or greater to 20 μA or less was used as an indication that the electrode tip was near the stratum opticum (13). Also, the direction and amplitude of stimulation-induced movements were used to predict the locations of the movement fields of neurons near the electrode tip (16). Thus, in order to isolate collicular neurons, auditory and visual targets were selected that would require movements having trajectories similar to those of stimulation-induced movements. Stimulation consisted of 40-ms trains of 0.25-ms pulses at 500 Hz. Current was varied between 10 and 70 μA.

Green light-emitting diodes (LEDs) subtending a visual angle of 12 min of arc were used as visual targets. A 20- to 20,000-Hz white-noise burst (80- to 90-dB sound pressure level) served as the auditory stimulus. The noise was projected from a 7.62-cm diameter speaker (Realistic, 40-1381) into a room lined either with heavy drapes or acoustic foam (Sonex, Illbruck). The monkeys were placed, with their heads fixed, in the center of a semicircular track (72-in. diam) that pivoted at both ends (Cal Tech Central Engineering Services). A speaker was attached to the track and a LED was placed in the center of the speaker. Computer-controlled stepping motors moved the speaker along the track to produce changes in azimuth and rotated the hoop to alter elevation (Fig. 1). Three stationary LEDs were mounted 24° apart in the horizontal plane and served as initial fixation targets.

A LSI-11/03 laboratory computer system was programmed to move targets to specified locations, control stimulus onset and duration, compare target and eye position, deliver reinforcements, and store eye position and interspike intervals on digital magnetic tape. Horizontal and vertical eye position signals were sampled at 3-ms intervals and successive interspike intervals were preserved with a resolution of 100 μs.

Behavioral tasks

Monkeys were maintained on a 21-h water-deprivation schedule for 6 days each week. Body weight and daily levels of fluid intake were carefully checked to monitor the hydration level and the

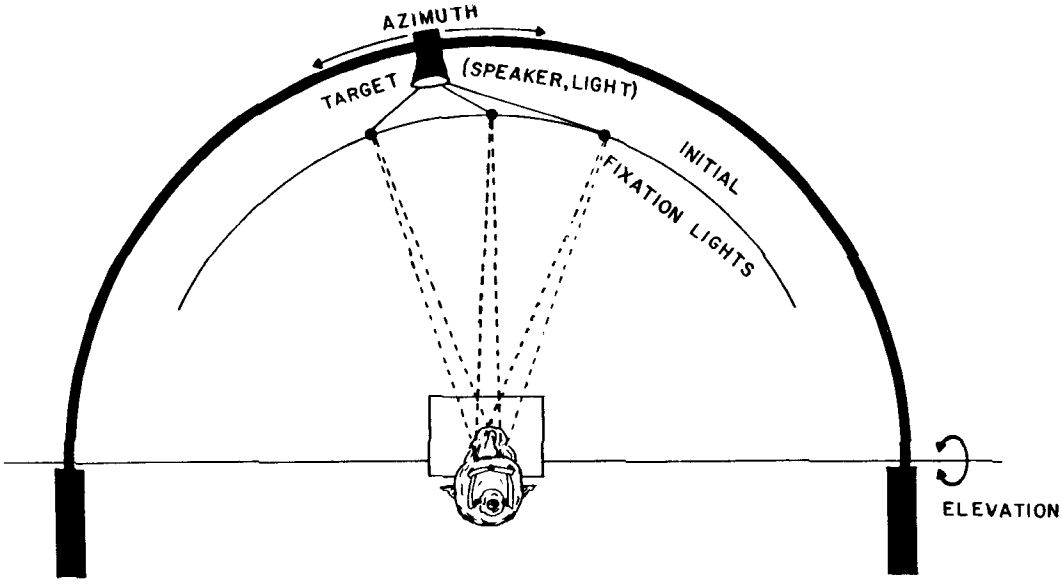

FIG. 1. Experimental apparatus. The subject was seated, with head fixed, in the center of a semicircular track that pivoted on both ends. A speaker with a light-emitting diode attached at the center was mounted on the track and could be moved by computer-controlled stepping motors to produce changes in the elevation or azimuth of the auditory or visual targets. Three initial fixation lights were placed 24° apart in the horizontal plane.

general health of the animals. Before each training or data collection session, the monkey was put into a primate chair and placed in an electrostatically shielded sound-attenuated chamber. The monkeys were initially trained to perform a direct saccade task (Fig. 2). Each trial began with the onset of a center fixation light. If the animal looked to the fixation target within 500 ms and maintained fixation for a variable period (up to 2 s), the fixation light was extinguished and, simultaneously, a peripheral visual target appeared. The monkey received a liquid reward (0.1 ml orange drink) for acquiring the peripheral target within 700 ms. Once this task was mastered, auditory targets were introduced. Initially, if the auditory target was not acquired within 700 ms, the LED mounted at the center of the speaker was illuminated allowing visually induced corrective saccades. As subjects became proficient in making saccades to the auditory target, the visual target was eliminated. Since target eccentricities as large as 40° were used and saccades to auditory targets were less accurate than saccades to visual targets (Jay and Sparks, in preparation),

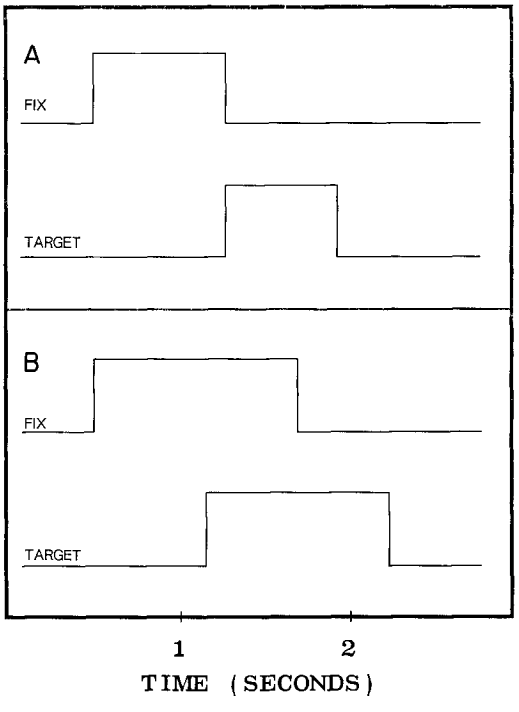

FIG. 2. Behavioral tasks. *A*: on direct saccade trials, the fixation light was extinguished simultaneously with the onset of a peripheral saccade target. *B*: on delayed saccade trials, the fixation light and saccade target overlapped in time (500–700 ms). Reward for both direct and delayed saccade tasks was contingent on maintaining fixation of the initial light as long as it was present (0.5–2.0 s) and then looking toward the peripheral target.

monkeys were rewarded for saccades within 8° of the auditory target and within 5° of the visual target. During all trials, the monkeys' heads were restrained so that interaural cues remained constant and only eye movements could be made to acquire the targets.

Subsequently, subjects were trained on visual and auditory delayed-saccade trials (Fig. 2) and on sensory probe trials (see Fig. 1, Ref. 6). Since most collicular neurons display a transient response to sensory stimuli, delayed-saccade trials were used to separate, temporally, sensory and motor activity. Sensory probe trials were used when trying to observe sensory responses in the absence of a saccade (see Ref. 6). On delayed-saccade trials (Fig. 2), one of the three fixation lights was illuminated and after a variable period (0.5–2.0 s), a peripheral auditory or visual target was presented while the fixation light was still activated. The fixation light and saccade target overlapped in time for 500–700 ms. Reward was contingent on maintaining fixation of the initial light until it was extinguished and then looking to the peripheral target within 700 ms. All electrophysiological data reported in this paper were collected while the monkeys performed the delayed saccade task.

Recording sessions

Once the electrode penetrated the colliculus, electrode depth was adjusted to isolate neurons with saccade-related activity while the animal generated, in total darkness, delayed saccades to auditory and visual targets. After isolating a cell, the optimal target position was quickly determined and two or three target positions were sampled (5–10 trials) with each of the three fixation directions. Target modality was randomly varied.

Data analysis

Eye movement onset and offset, automatically defined using velocity criteria, were verified for each trial. The criteria were adjusted as necessary to define saccades with unusual velocity profiles. For up to two movements per trial (primary and corrective saccades), the latency, size, duration, peak velocity, and acceleration time of the saccades as well as the final error for the total eye movement and for the horizontal and vertical components were stored. The time between the first and second saccades, the number of spikes, peak firing rate, duration, and lead time of both the sensory and motor responses were also computed and stored.

To see if the parameters of the motor burst occurring when saccades were made to auditory targets differed from those observed when saccades were made to visual targets, a program scanned all saccades generated while a single cell was being recorded and selected the best matches between the trajectories of saccades to auditory and visual tar-

gets. Matches in which the difference in total amplitude between the two movements was >30% of the largest saccade were eliminated from the analysis. Any remaining matches in which the endpoints of the saccade vector differed by more than 5° were also discarded. For these matched pairs of saccades, a correlation coefficient was calculated to determine the relationship between differences in peak saccadic velocity for auditory and visual saccades and differences in peak firing rate during the same two trials.

RESULTS

The premotor activity of 72 neurons in the primate SC was monitored while monkeys generated comparable saccades to auditory and visual targets. The sensory responsiveness and motor properties of these cells are summarized in Table 1.

Most cells (79%) produced a premotor burst of activity prior to saccades in their movement field, regardless of target modality. An example of the activity of a SRB cell discharging before saccades to either sounds or lights is shown in Fig. 3. In all panels, the saccade target was located 16° to the left and 10° above the central fixation stimulus. Auditory trials are illustrated on the top (Fig. 3*A*) and visual trials on the bottom (Fig. 3*B*). When the animal was viewing the center fixation light (middle column), a high-frequency burst of activity preceded saccades initiated by either auditory or visual targets. The peak firing rate of the premotor burst was similar for both trial types. When the animal fixated the 24° right initial target, a 40° horizontal and 10° upward saccade was required to look to the saccade target. The cell's discharge was markedly reduced (150 vs. 900 spikes/s), compared with trials with saccades from the central fixation point, indicating that these large movements were on the edge of the movement field. Trials initiated when the monkey was fixating 24° to the left of center are shown in the left column. The acquisition saccade under these conditions was 8° right and 10° up. Little saccade-related activity occurred prior to these rightward saccades regardless of target modality. Since auditory targets are localized in head coordinates, neurons might have been encountered that discharged whenever a saccade (regardless of direction or amplitude) directed gaze to a particular position in space. According to this hypothesis, the cell illustrated in Fig. 3 (generating a vigorous burst when looking from center fixation to a target located 16° to the left and 10° upward) would be expected to generate a vigorous burst of activity when a saccade was made to the same target location from either the left or right fixation positions. Neither this cell nor any other cell studied displayed this response property. Instead, for all cells studied, the magnitude of the saccade-related discharge was independent of original fixation position and was related to the direction and amplitude of the saccade. For example, the cell illustrated in Fig. 3 generated an equally vigorous burst on trials with fixation of the left or right LEDs if a 16° leftward and 10° upward saccade was required for target acquisition (not illustrated).

TABLE 1. *Sensory responsiveness and motor properties of collicular neurons*

		Sensory Responses			Motor Properties		
Cell Type	*n*	V/A	V	A	V/A	V	A
SRB	13				12	1	0
V-M	59	2	57	0	45	13	1
Total	72						

n, No. of neurons; SRB, saccade-related burst cells; V-M, visual-motor cells; V/A, respond to visual or auditory stimuli (sensory) or discharge before saccades to visual or auditory targets (motor); V, respond to visual but not auditory stimuli (sensory); discharge before saccades to visual but not auditory targets (motor); A, respond to auditory but not visual stimuli (sensory); discharge before saccades to auditory but not visual targets (motor).

Of the 13 SRB cells recorded while the monkeys made acoustically or visually triggered saccades of comparable trajectories, all but one discharged before saccades to either type of target. The remaining cell burst before saccades to visual but not auditory targets. No cells with strictly motor properties were isolated that discharged prior to saccades to auditory but not to visual targets.

V-M cells display a discrete burst of activity time-locked to stimulus onset and a second, motor burst immediately preceding the acquisition saccade. Of the 59 V-M cells recorded during both auditory and visual trials, 45 generated a saccade-related burst before saccades on either trial type. While the motor portion of the activity of these cells was generally shared by both the auditory and visual

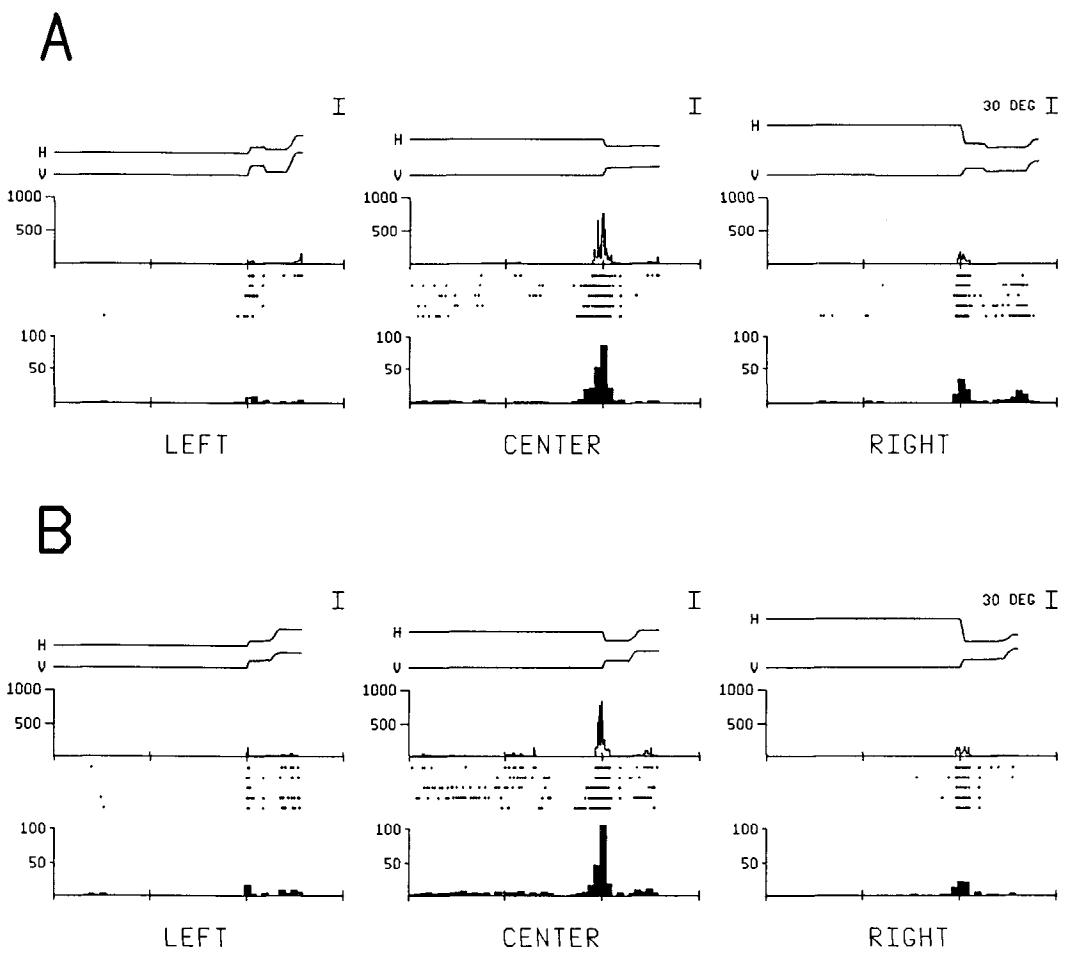

FIG. 3. Activity of a saccade-related burst (SRB) cell that discharged before saccades to auditory or visual targets. For all data shown, the saccade target was 16° left and 10° up from center. The *top two traces* in each panel represent horizontal (H; up, right) and vertical (V; up, up) eye position for a single trial and are followed by an instantaneous spike histogram of the neuronal activity recorded during the same trial. Next, the firing patterns for that trial and 4 others are shown as rasters aligned with saccade onset. The *bottom trace* in each panel is a cumulative histogram of the neural activity represented in the rasters. The total time represented on the *abscissa* is 3 s; the onset of the saccade target occurred at the 1-s mark. On these delayed saccade trials, the signal to initiate the eye movement (the offset of the fixation light) occurred 500–700 ms after the target was first presented. *A*: auditory trials. *B*: visual trials. *Left*: trials with initial fixation of the 24° left light-emitting diode (LED). *Center*: trials with center fixation. *Right*: trials with fixation of the 24° right LED.

systems, the initial sensory burst was not. Two cells displayed a discrete sensory burst in response to the presentation of either auditory or visual targets; the remaining 57 cells generated an initial sensory response on visual trials only.

The activity of a cell with a visual, but not auditory, response and a premotor discharge before both auditory and visual saccades is illustrated in Fig. 4. For the trials shown, the targets were presented 12° to the left and 14° above the center fixation light. On visual trials (Fig. 4*B*), sensory and motor responses occurred when the center or right initial fixation stimuli were employed. The largest visual response was obtained on trials with center fixation; a reduced response was evident on trials with right fixation. Neither sensory nor motor bursts occurred on trials with a 24° leftward fixation when a rightward, rather than a leftward, saccade was required. In contrast to the biphasic response profile seen with delayed

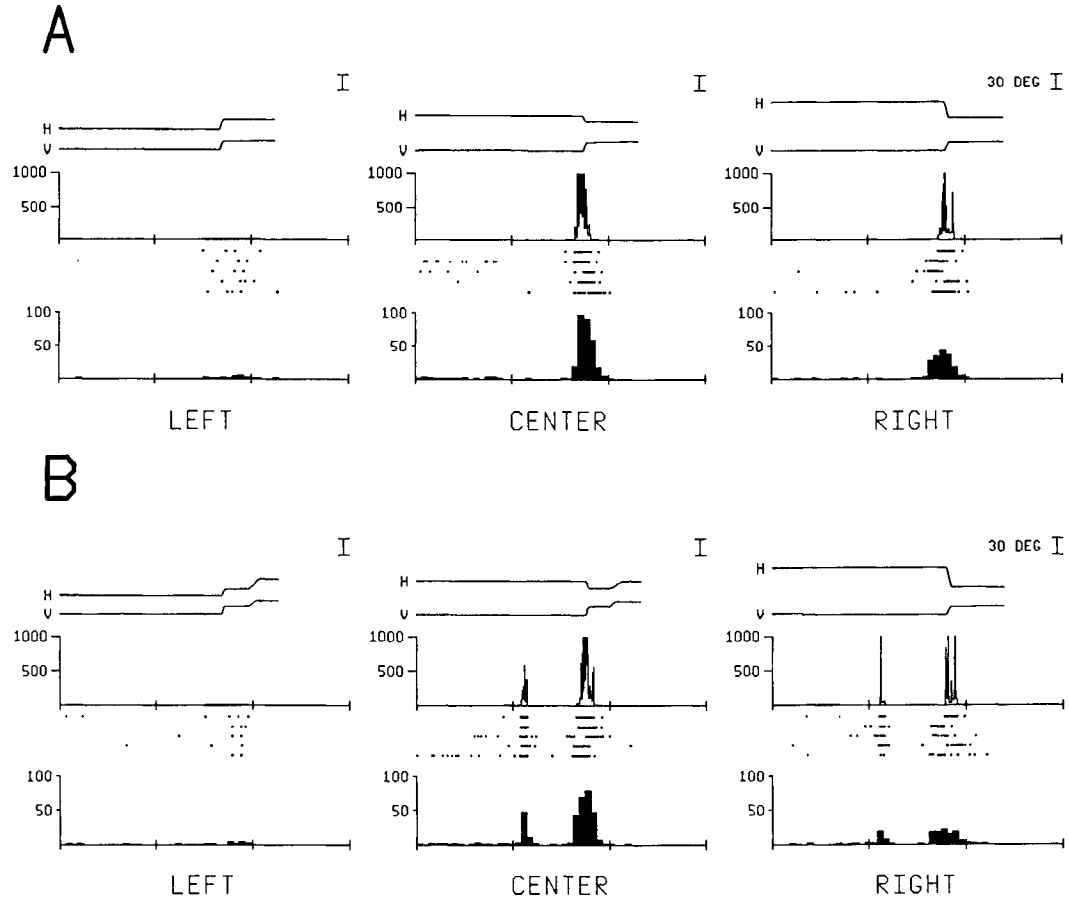

FIG. 4. Activity of a visual-motor cell that responded to visual, not auditory, stimuli but burst before saccades to either auditory or visual targets. See Fig. 3 to identify traces. *A*: auditory trials. *B*: visual trials. The saccade target was 12° left, 14° above center for all trials.

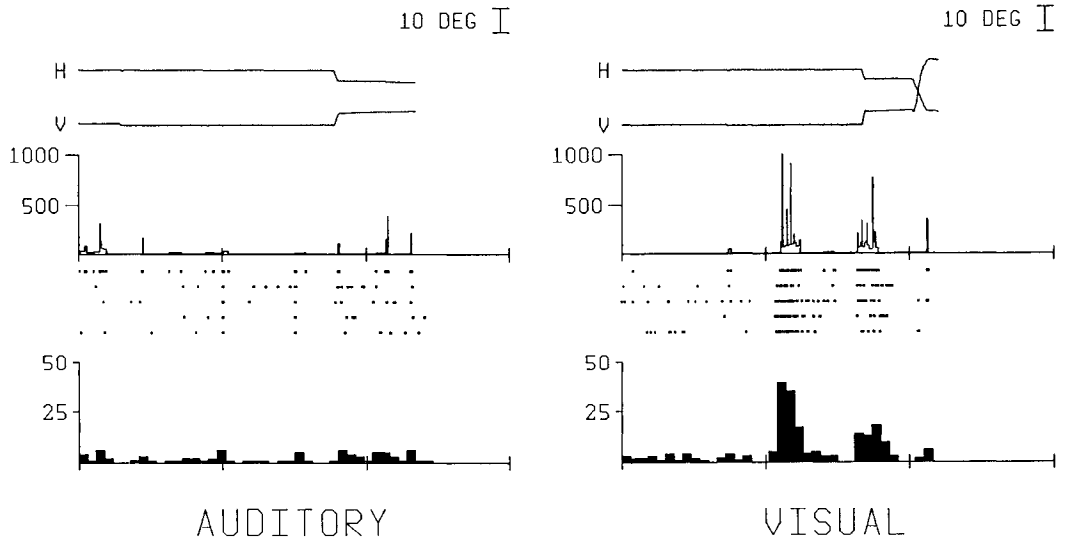

FIG. 5. Example of a visual-motor cell that generated sensory and motor bursts on visual trials (*right*) but displayed neither sensory-induced nor premotor activity on auditory trials (*left*). Auditory and visual trials are matched for target location (4° left, 4° up) and for saccade direction and amplitude.

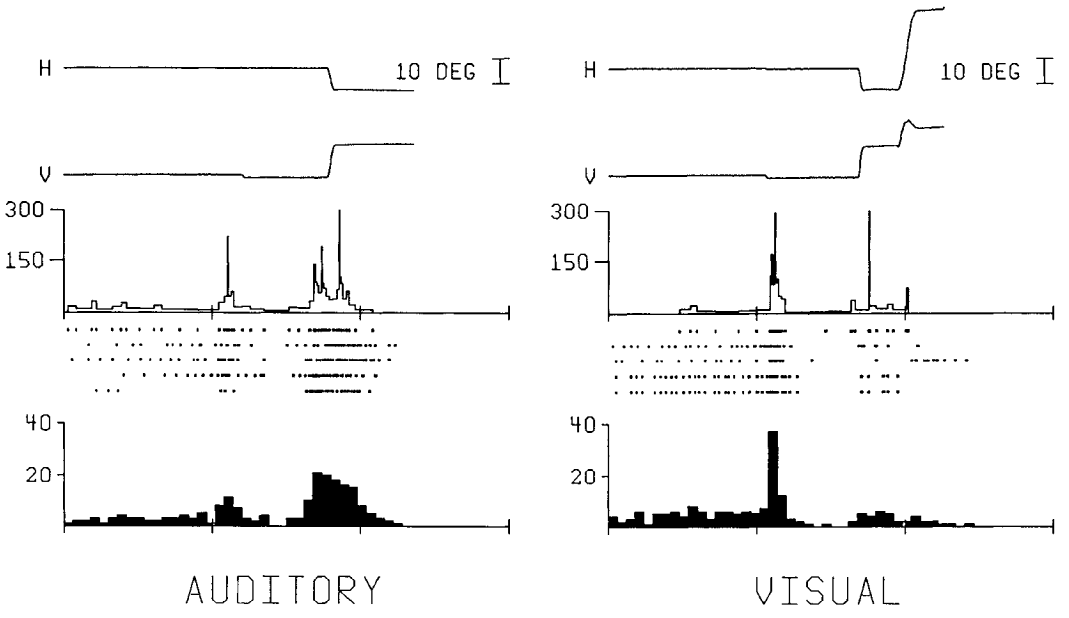

FIG. 6. Example of a cell that displayed presaccadic motor activity only on auditory trials. Target location: 10° left, 10° up. On matched visual trials (*right*), only the sensory response was observed.

saccades to visual targets (Fig. 4*B*), only the second motor burst was observed on auditory trials (Fig. 4*A*).

Some cells produced premotor bursts for saccades to targets of one but not the other modality. Of the 59 V-M cells studied, 13 were active only during visual trials. With these cells, neither a sensory nor a motor burst occurred when saccades were made to auditory targets. An example of such a cell is illustrated in Fig. 5. A burst of activity occurred in response to the presentation of a visual target 4° to the left and 4° above the initial fixation stimulus (right panel). A second burst occurred just prior to the visually triggered saccade. On auditory trials, neither sensory nor motor

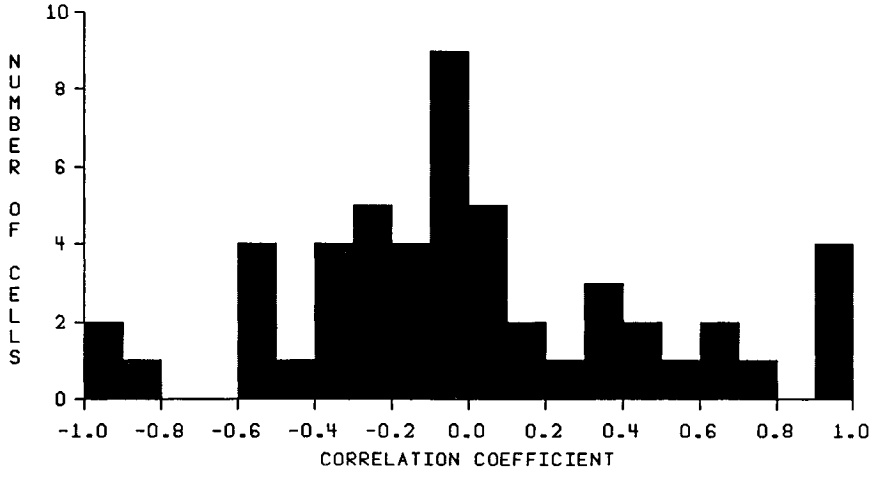

FIG. 7. Distribution of correlation coefficients between the differences in saccadic velocity and differences in peak firing rate on auditory and visual trials matched for direction and amplitude of saccades for 50 superior colliculus cells.

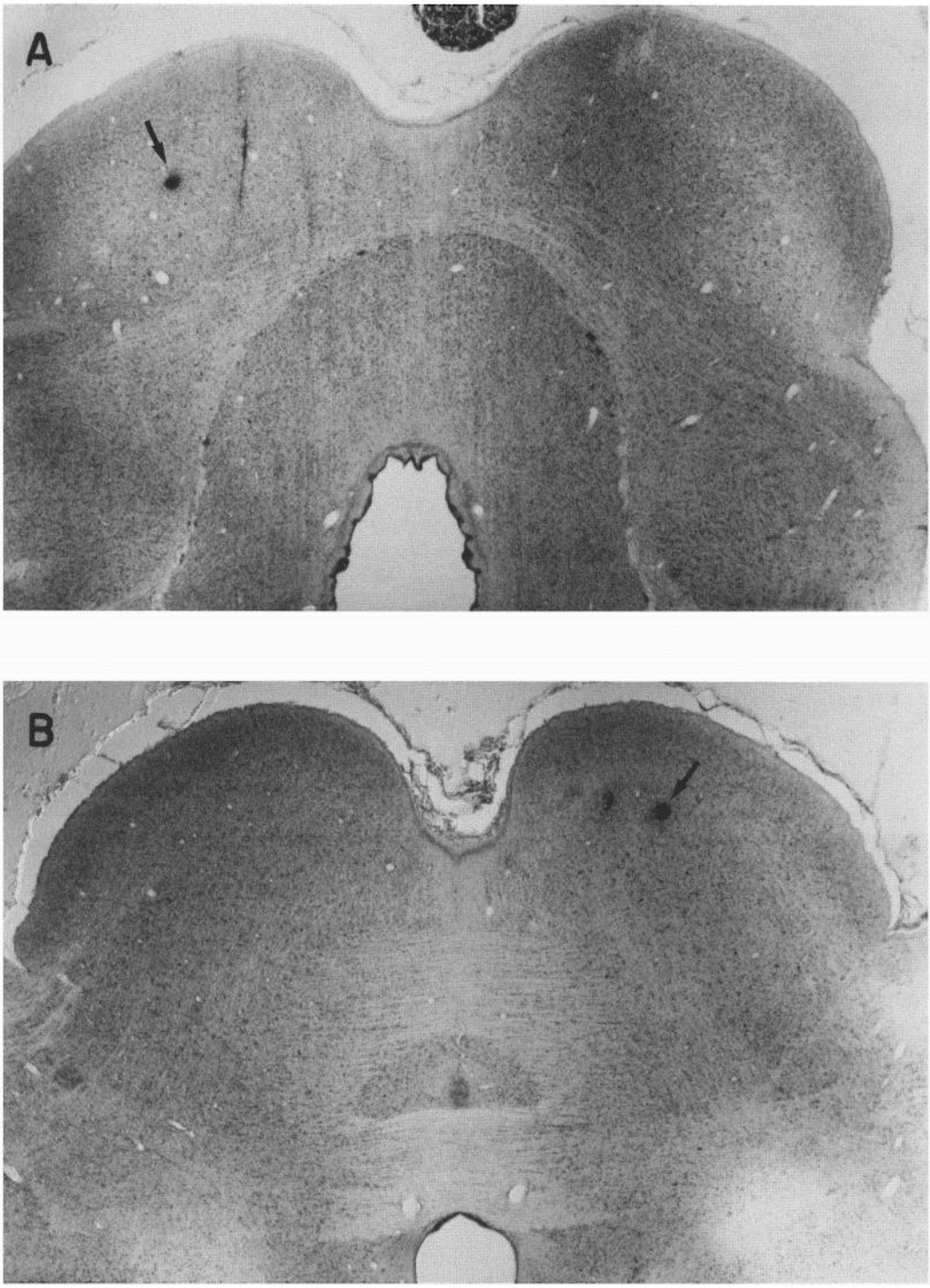

FIG. 8. Lesions (indicated by *arrows*) placed at the site of a saccade-related burst cell (*A*) and a visual-motor cell (*B*).

bursts were evident. Most cells of this type were responsive to stimuli activating central regions of the retina and discharged before saccades of small amplitude.

In the entire sample of cells with premotor activity recorded during matched auditory and visual saccades, only one burst exclusively before saccades to auditory targets. The activity of this cell is illustrated in Fig. 6. A sensory response occurred following presentation of either auditory or visual stimuli but the increased firing coupled to saccade onset occurred only on auditory trials. The apparent increase in spike activity associated with saccades on visual trials is a release from inhibition; presaccadic activity levels do not exceed control firing rates. It should be noted that for this cell, the peak firing rate of the saccade-related burst was <200 spikes/s; the motor bursts of most collicular neurons reach much higher peak instantaneous frequencies (up to 1,000 spikes/s).

Although the premotor bursts of most cells active before auditory and visual trials were approximately the same under both conditions (see Figs. 3 and 4), a few cells produced motor bursts that differed depending on the modality of the stimulus, even if the amplitude and direction of subsequent eye movements were comparable. For both subjects, the peak velocity of saccades to auditory targets was significantly lower than the peak velocity of saccades to visual targets (Jay and Sparks, in preparation). To determine if velocity differences between auditory and visual saccades were correlated with the firing pattern of collicular burst cells, matched pairs of saccades to visual and auditory targets were selected. For these matched movements, correlation coefficients were calculated between the difference in peak velocity and difference in peak firing rate for each cell. For the sample, no consistent relationship was found. Although differences in the activity of a few cells were highly correlated with velocity differences (Fig. 7), the correlation coefficients for most cells were near zero, with approximately as many units having positive correlations as negative ones.

Lesions made at sites where cells with bursts preceding saccades were isolated are shown in Fig. 8. Figure 8*A* shows the lesion made at the site of a SRB cell discharging before saccades to auditory or visual targets. A lesion at the site of a V-M cell with a visual sensory component and combined auditory/visual premotor burst is shown in Fig. 8*B*. Both lesions are in the intermediate gray.

DISCUSSION

Most collicular cells that discharge before saccades to visual targets also discharge before spontaneous saccades (10, 16, 20, 24) and, although not tested as frequently, some fire before the quick phases of optokinetic and vestibular nystagmus (16). Since these cells discharge before spontaneous saccades within their movement field, it may not seem remarkable that they also discharge before saccades to auditory targets. However, the finding that a cell bursts before spontaneous saccades does not necessarily indicate that the same cell will discharge before saccades to auditory targets. Spontaneous saccades are so named because the experimenter cannot identify the external or internal stimulus that initiated the movement. Since the stimulus that initiated the movement is unknown, there is no basis for arguing that the cell does or does not discharge before saccades to a particular sensory cue. It was necessary, therefore, to determine, explicitly, whether or not collicular neurons participate in the initiation of saccades to auditory targets and, if so, whether these neurons are the same neurons that discharge before saccades to visual targets.

Thus the major goal of this experiment was to determine whether or not neurons in the SC that discharge before saccades to visual targets also discharge before saccades to auditory targets. Since localization of auditory targets is based on binaural cues and the localization of visual targets is based, initially, on the locus of retinal stimulation, different premotor pathways could be utilized by the auditory and visual systems. If so, then it would be expected that some collicular neurons would burst before visually triggered saccades and others would discharge before saccades to auditory targets. If, however, auditory and visual signals have been converted into the same coordinates and are sharing a motor circuit, then each collicular neuron with saccade-related activity should discharge before movements to either auditory or visual targets. Our findings support the second alternative. Seventy-nine percent of cells with saccade-re-

lated activity burst before both visually triggered and sound-induced saccades. Thus, at the level of the SC, sensory signals have been converted into a common coordinate system and are sharing a motor pathway to other oculomotor centers.

Since auditory targets are localized in head coordinates, motor commands to orient the eyes toward the source of a sound could also be generated in head coordinates. If the head and body were stationary, a neuron carrying a motor command encoded in head coordinates would discharge before all eye movements that directed gaze to a specific location in space, regardless of the direction and amplitude of the movement. This was not true of neurons in the SC that burst before saccades to auditory targets. Varying initial fixation position, and thereby changing the amplitude and/or direction of saccades required to look to a target, significantly affected the probability and magnitude of presaccadic discharges. Collicular neurons discharging before saccades to auditory or visual targets burst maximally before saccades of a particular direction and amplitude regardless of the position of the eye in the orbit. The presaccadic activity of neurons in the SC represents a command to correct for a particular discrepancy between current and desired eye position (motor error) rather than a command to move the eyes to a particular orbital position. Thus, by the time they reach SRB cells in the SC, auditory signals, originally encoded in head coordinates, have been translated into saccadic motor error coordinates. With the head fixed, the trajectory of the eye movement required to look to an auditory target (motor error) is the difference between the current direction of gaze and the location of the target in space, a computation requiring precise signals of head position and the current position of the eye in the orbit.

Twelve of the 13 SRB cells studied discharged before saccades to auditory or visual targets. The one cell that did not do so was probably a visually triggered movement cell (11), a subclass of burst cells that fires before saccades to visual targets but not before spontaneous saccades of the same trajectory. Axons of SRB neurons are thought to comprise a major efferent pathway from SC to the paramedian pontine reticular formation (9), a region of the brain stem necessary for all types of conjugate horizontal eye movements (2, 8, 12). Moreover, the discharge of SRB cells is thought to serve as a trigger input (21) to the brain stem neuronal network (14) generating saccades. The findings of this paper suggest that SRB cells trigger saccades to auditory as well as visual targets.

The convergence of auditory and visual sensory and motor signals does not occur for all collicular cells. Thirteen of 59 V-M cells generated a motor burst only before saccades to visual targets. One cell displayed a saccade-related burst only before saccades to auditory targets. Most of the cells that did not discharge before saccades to auditory targets burst maximally before small amplitude movements. Few of the auditory receptive fields described in the following paper (6) were found to be centered near the fixation position. This poor representation of auditory signals near current eye position and the general lack of responsiveness of motor cells prior to small sound-initiated saccades could be responsible for the long latency of small amplitude eye movements to auditory targets (Jay and Sparks, in preparation). Alternatively, the activity of cells discharging only before saccades to visual targets may be combined with the activity of cells discharging only before saccades to auditory targets to form a new population of neurons that discharge before saccades to either type of target.

Nor was there a complete convergence of auditory and visual signals in the sensory responses of collicular neurons. The sensory bursts of most V-M cells were exclusively visual, even in those cells that produced motor bursts prior to auditory saccades. This finding is in marked contrast with results reported in the following paper (6). A high percentage of neurons in deeper layers of the SC that respond to auditory stimuli are also responsive to visual stimuli. The finding that most V-M cells fail to respond to auditory stimuli indicates that the sensory burst of V-M cells is not necessary for the occurrence of the motor burst. This conclusion is also supported by the finding that deactivation of the striate cortex obliterates the visual responsiveness of neurons in the intermediate layers of the primate SC without affecting the presaccadic motor discharge of neurons in this layer (17). The exact role of V-M cells in the control of saccadic eye movements is unknown. For many of these cells, the configurations of the sensory and motor

components of the discharge are remarkably similar. Moreover, the motor burst may occur in the absence of a sensory response (see above) or the sensory response may occur in the absence of a motor burst (19). Thus, unless the discharge of V-M cells is compared with that of purely motor or purely sensory cells, it is difficult to understand how neurons receiving inputs from V-M cells effectively utilize the transmitted signals.

For most collicular neurons studied, we obtained low correlations between changes in peak firing rate and differences in saccadic velocity on auditory and visual trials matched for direction and amplitude. This suggests that, like other parameters of saccadic eye movements (direction, amplitude, etc), information about saccadic velocity is unlikely to be encoded by the discharge of individual collicular neurons (21). However, there was considerable trial-to-trial variability in the direction and amplitude of saccades to the same auditory target, and we were unable to obtain a large number of precise matches for each cell. This is particularly bothersome since two movements that differ slightly in direction and/or amplitude fall on different locations in the movement field of the cell, and variations in discharge parameters may be associated with differences in trajectory rather than differences in velocity. This question needs to be reexamined in a situation in which the trajectories of auditory saccades are computed on-line so that visual targets providing exact matches can be selected. However, since fewer neurons are active before saccades to auditory targets and since saccades to auditory stimuli usually have lower velocities, saccadic velocity may be determined by the size of the population of collicular neurons active before a particular movement.

Results of the present experiment support the hypothesis that the SC is a site where sensory signals, originally encoded in different coordinates, converge and are translated into a common motor command: a command to correct for saccadic motor error. It is not known, however, whether this coordinate conversion occurs within the SC or whether sensory signals reaching the intermediate layers of the SC have already been translated into motor error coordinates. The experiment described in the following paper (6) addresses these questions.

ACKNOWLEDGMENTS

We thank I. Ragland, K. Hamrick, and B. Deich for technical assistance and K. Pearson and H.-T. Chiu for computer programming.

This work was supported by National Eye Institute Grants R01 EY-01189 and P30 EY-03039.

Present address of M. Jay: University of South Carolina School of Medicine, Columbia, South Carolina, 29208.

Received 13 March 1986; accepted in final form 21 August 1986.

REFERENCES

1. FUCHS, A. F. AND ROBINSON, D. A. A method for measuring horizontal and vertical eye movement chronically in the monkey. *J. Appl. Physiol.* 21: 1068–1070, 1966.
2. HENN, V. AND COHEN, B. Coding of information about rapid eye movements in the pontine reticular formation of alert monkeys. *Brain Res.* 108: 307–325, 1976.
3. HIKOSAKA, O. AND WURTZ, R. H. Modification of saccadic eye movements by GABA-related substances. I. Effect of muscimol and bicuculline in monkey superior colliculus. *J. Neurophysiol.* 53: 266–291, 1985.
4. JAY, M. F. AND SPARKS, D. L. Auditory receptive fields in the primate superior colliculus that shift with changes in eye position. *Nature Lond.* 309: 345–347, 1984.
5. JAY, M. F. AND SPARKS, D. L. Auditory and saccade-related activity in the superior colliculus of the monkey. *Soc. Neurosci. Abstr.* 12: 951, 1982.
6. JAY, M. F. AND SPARKS, D. L. Sensorimotor integration in the primate superior colliculus. II. Coordinates of auditory signals. *J. Neurophysiol.* 57: 35–55, 1987.
7. JUDGE, S. J., RICHMOND, B. J., AND CHU, F. C. Implantation of magnetic search coils for measurement of eye position: An improved method. *Vision Res.* 20: 535–538, 1980.
8. KELLER, E. L. Participation of medial pontine reticular formation in eye movement generation in monkey. *J. Neurophysiol.* 37: 316–320, 1974.
9. KELLER, E. L. Colliculoreticular organization in the oculomotor system. In: *Progress in Brain Research. Reflex Control of Posture and Movement,* edited by R. Granit and O. Pompeiano. Amsterdam: Elsevier, 1979, p. 725–734.
10. MAYS, L. E. AND SPARKS, D. L. Dissociation of visual and saccade-related responses in superior colliculus neurons. *J. Neurophysiol.* 43: 207–231, 1980.
11. MOHLER, C. W. AND WURTZ, R. H. Organization of monkey superior colliculus: intermediate layer cells discharging before eye movements. *J. Neurophysiol.* 39: 722–744, 1976.

12. RAPHAN, T. AND COHEN, B. Brainstem mechanisms for rapid and slow eye movements. *Annu. Rev. Physiol.* 40: 527–552, 1978.
13. ROBINSON, D. A. Eye movements evoked by collicular stimulation in the alert monkey. *Vision Res.* 12: 1795–1808, 1972.
14. ROBINSON, D. A. Oculomotor control signals. In: *Basic Mechanisms of Ocular Motility and Their Clinical Implications*, edited by G. Lennerstrand and Bach-y-Rita. Oxford: Pergamon, 1975, p. 337–374.
15. 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.
16. SCHILLER, P. H. AND STRYKER, M. Single-unit recording and stimulation in superior colliculus in the alert rhesus monkey. *J. Neurophysiol.* 35: 915–924, 1972.
17. SCHILLER, P. H., STRYKER, M., CYNADER, M., AND BERMAN, N. Response characteristics of single cells in the monkey colliculus following ablation or cooling of visual cortex. *J. Neurophysiol.* 37: 181–194, 1974.
18. SCHILLER, P. H., TRUE, S. D., AND CONWAY, J. L. Deficits in eye movements following frontal eye-field and superior colliculus ablations. *J. Neurophysiol.* 44: 1175–1189, 1980.
19. SPARKS, D. L. Functional properties of neurons in the monkey superior colliculus: Coupling of neuronal activity and saccade onset. *Brain Res.* 156: 1–16, 1978.
20. SPARKS, D. L., HOLLAND, R., AND GUTHRIE, B. L. Size and distribution of movement fields in the monkey superior colliculus. *Brain Res.* 113: 21–34, 1976.
21. SPARKS, D. L. AND MAYS, L. E. Movement fields of saccade-related burst neurons in the monkey superior colliculus. *Brain Res.* 190: 39–50, 1980.
22. STEIN, B. E., MAGALHÃES-CASTRO, B., AND KRUGER, L. Relationship between visual and tactile representations in cat superior colliculus. *J. Neurophysiol.* 39: 401–419, 1976.
23. WICKELGREN, B. G. Superior colliculus: some receptive field properties of bimodally responsive cells. *Science Wash. DC* 173: 69–72, 1971.
24. WURTZ, R. H. AND GOLDBERG, M. E. Activity of superior colliculus in behaving monkey. III. Cells discharging before eye movements. *J. Neurophysiol.* 35: 575–596, 1972.
25. ZAHN, J. R., ABEL, L. A., AND DELL'OSSO, L. F. Audio-ocular response characteristics. *Sensory Processes* 2: 32–37, 1978.
26. ZAMBARBIERI, D., SCHMID, R., PRABLANC, C., AND MAGENES, G. Characteristics of eye movements evoked by the presentation of acoustic targets. In: *Progress in Oculomotor Research*, edited by A. Fuchs and W. Becker. Amsterdam: Elsevier/North-Holland, 1981, p. 559–566.