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

Sensorimotor Integration in the Primate Superior Colliculus. II. Coordinates of Auditory Signals

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. Based on the findings of the preceding paper, it is known that auditory and visual signals have been translated into common coordinates at the level of the superior colliculus (SC) and share a motor circuit involved in the generation of saccadic eye movements. It is not known, however, whether the translation of sensory signals into motor coordinates occurs prior to or within the SC. Nor is it known in what coordinates auditory signals observed in the SC are encoded.

2. The present experiment tested two alternative hypotheses concerning the frame of reference of auditory signals found in the deeper layers of the SC. The hypothesis that auditory signals are encoded in head coordinates predicts that, with the head stationary, the response of auditory neurons will not be affected by variations in eye position but will be determined by the location of the sound source. The hypothesis that auditory responses encode the trajectory of the eye movement required to look to the target (motor error) predicts that the response of auditory cells will depend on both the position of the sound source and the position of the eyes in the orbit.

3. Extracellular single-unit recordings were obtained from neurons in the SC while monkeys made delayed saccades to auditory or visual targets in a darkened room. The coordinates of auditory signals were studied by plotting auditory receptive fields while the animal fixated one of three targets placed 24° apart along the horizontal plane.

4. For 99 of 121 SC cells, the spatial location of the auditory receptive field was significantly altered by the position of the eyes in the orbit. In contrast, the responses of five sound-sensitive cells isolated in the inferior colliculus were not affected by variations in eye position.

5. The possibility that systematic variations in the position of the pinnae associated with different fixation positions could account for these findings was controlled for by plotting auditory receptive fields while the pinnae were mechanically restrained. Under these conditions, the position of the eyes in the orbit still had a significant effect on the responsiveness of collicular neurons to auditory stimuli.

6. The average magnitude of the shift of the auditory receptive field with changes in eye position (12.9°) did not correspond to the magnitude of the shift in eye position (24°). Alternative explanations for this finding were considered. One possibility is that, within the SC, there is a gradual transition from auditory signals in head coordinates to signals in motor error coordinates. In this case, cells with differing amounts of receptive field shift would represent different points in this process.

7. These and other results can best be explained by assuming that the intermediate and deeper layers of the primate SC are organized in motor error coordinates. Motor error, the change in eye position required to look to a target, is encoded anatomically since it is the site of activity within the colliculus that specifies saccade direction and amplitude. Accordingly, inputs to the SC must specify, by activating a particular subset of neurons, the change in eye position required to look to a target. This requires a dynamic map of sensory activity within the SC. With each change in eye position, the site of sensory-induced activity shifts to a new location, a location specifying the metrics of the movement that will direct gaze to the target location.

INTRODUCTION

The intermediate and deeper layers of the superior colliculus (SC) contain neurons responsive to auditory, visual, and somatosensory stimuli. Each sensory neuron has a spatially restricted receptive field and neurons are arranged, anatomically, so that orderly maps of sensory space are found within these layers. The topographical maps of auditory, somatosensory, and visual space appear to be aligned

correspondence found between these maps is seen by comparing the spatial location of receptive fields of tactile or auditory cells with the receptive fields of retinotopically organized visual cells in the superficial layers (5, 7, 8, 19, 20, 33–36).

The observed correspondence between sensory maps in the SC of anesthetized and/or paralyzed subjects is curious because, at earlier points in the sensory pathways, the spatial location of a stimulus is encoded differently for each sensory system. The neural code for the location of a visual stimulus is based on information about the position of the eyes in the orbits and the locus of retinal stimulation. In contrast, the location of sound sources is encoded using head-centered cues such as interaural differences in the timing and intensity of incoming sound waves. Tactile stimuli are localized in a third body-centered reference system. The apparent alignment of auditory, visual, and somatosensory maps in the SC implies that these sensory signals have been translated into a common coordinate system. However, as noted by Pöppel (27), this hypothesis cannot be tested in the anesthetized animal because, under these conditions, the axes of the head-centered auditory system, the retinotopic visual system, and body-centered somatosensory system are aligned. In the present study, the receptive fields of neurons responsive to auditory and visual stimuli were plotted while the eye position of trained alert monkeys was systematically varied to introduce disparities between retinotopic and head-centered coordinates. If the auditory and visual signals recorded from collicular neurons have not been transformed (i.e., remain in head or retinal coordinates), and if the orderly maps of sensory space are static, then the auditory and visual maps would not remain aligned when the position of the eyes is varied.

A possibility less frequently considered is that the signals of collicular neurons responsive to sensory stimuli are encoded in motor, rather than sensory, coordinates. Mays and Sparks (22) reported evidence that visually responsive neurons in the intermediate layers of the SC provide a signal of saccadic motor error, the amplitude and direction of the eye movement required to look to a target. Quasi-visual (QV) cells in the intermediate layers of the primate SC are visually responsive and appear, under usual test conditions, to respond to stimuli activating specific retinal regions. But when a double saccade task is used to dissociate the site of retinal stimulation from the eye movement required for target acquisition, the activity of QV cells is independent of the site of retinal stimulation and, instead, represents a signal of motor error.

In experiments described in the preceding paper (15), we recorded from saccade-related burst neurons in the intermediate layers of the SC and found 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 premotor pathway for the generation of saccadic eye movements. The major purpose of the experiments described in this paper was to determine if auditory signals observed in the SC are encoded in sensory (head) or motor (motor error) coordinates. Neurons responsive to auditory stimuli, found in deeper layers of the SC (below the cells with saccade-related activity), have not been extensively studied in the monkey. If auditory signals are organized in head coordinates, then in our experiments in which the head is fixed, the discharge of acoustically responsive neurons should be independent of initial fixation position and depend entirely on the azimuth and elevation of the sound source. However, if auditory signals have been translated into motor error coordinates, then the response of collicular neurons to acoustic stimuli should depend on the trajectory of the movement required to look to the stimulus and, therefore, be sensitive to both the position of the speaker in space and the position of the eyes in the orbit.

For most auditory cells tested, eye position had a distinct effect on their response to sounds. The auditory receptive fields moved when eye position was changed. The neurons

were maximally sensitive to sound stimuli requiring a saccade of a particular direction and amplitude to look to the stimulus. We conclude that auditory and visual signals observed in the deeper layers of the primate SC do not represent a static map of sensory space, but that these signals have been remapped into motor coordinates. The map of sensory activity is a dynamic one; with each change in eye position, the site of sensory-induced activity shifts to a location that encodes, anatomically, the trajectory of the movement required to look to the selected target.

Preliminary reports of these findings have appeared elsewhere (16, 17).

METHODS

The same two rhesus monkeys used in the experiments described in the previous paper (15) served as subjects. Surgical procedures, microelectrode recording and microstimulation techniques, methods for measuring eye position, and behavioral training procedures are described in the preceding paper (15).

Trial types

DELAYED-SACCADE TRIALS. Receptive fields were plotted while monkeys performed, in total darkness, a delayed-saccade task (see Fig. 2, Ref. 15). At the beginning of each trial, one of the three fixation lights, 24° apart along the horizontal plane, was activated. Then an eccentric auditory or visual saccade target was presented while the first light remained illuminated. To receive the liquid reward, the monkey had to maintain fixation of the first target until it was extinguished and then look to the saccade target (see Ref. 22 for details). By imposing a delay between the appearance of the eccentric stimulus and the saccade to it, the onset of sensory activity could be easily distinguished from the onset of motor activity.

SENSORY PROBE TRIALS. A sensory probe task (Fig. 1) was designed to determine whether neural activity temporally linked to stimulus onset would appear if saccades to the peripheral stimuli failed to occur. As with the delayed-saccade task, probe trials began with the onset of one of the three initial visual fixation lights and, after a variable delay (0.5–2.0 s), a peripheral auditory or visual target was presented. In contrast to the delayed-saccade trials, on probe trials both the fixation light and saccade target were extinguished simultaneously. An eye movement was not required for reward; reinforcement was delivered if the monkey maintained fixation of the initial light during the entire trial. If the trial sequence consisted of only sensory probe trials with the stimulus never serving as a saccade target, habituation of the neural response occurred (11). To avoid this problem, a small percentage of delayed-saccade trials was intermixed with probe trials.

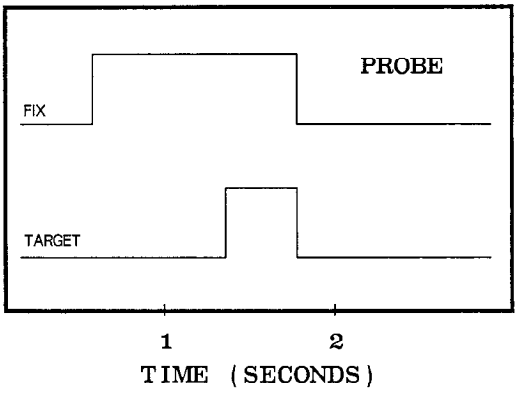

FIG. 1. Sensory probe task. After the animal acquired the fixation target and maintained fixation for a variable period, an eccentric target was presented briefly while the initial fixation light remained illuminated. Then both the fixation target and eccentric target were extinguished simultaneously. Reward was contingent on maintaining fixation of the initial light for the duration of the trial. A saccade to the peripheral target was not required.

Data collection procedures

Since visually induced activity was more prevalent in the primate SC than auditory activity, visual (10%) and auditory (90%) trials were intermixed while searching for sound-sensitive cells. Once a cell was isolated, the optimal target position was quickly determined and the speaker was maintained at that elevation while the horizontal extent of the receptive field was plotted in 10° increments. Since hoop rotation and speaker movement imposed a relatively long delay in the data collection process, the target was usually kept at one position, relative to the head, while the initial fixation direction was randomly varied until data were collected on 5–10 trials from each fixation direction. Then the target was moved to another location and the process repeated. Control experiments in which fixation position and target location were varied independently indicated that this procedure did not significantly affect the receptive field plots.

For most cells, the horizontal extent of the auditory receptive fields was plotted first, and then the visual fields were determined. For seven cells, the vertical extent of the auditory and visual receptive fields was plotted by keeping the speaker at the optimal horizontal position and varying target elevation. In some cases, the fields were plotted using probe trials or the response to the presentation of simultaneous auditory and visual targets was de-

termined. For 22 cells, the auditory receptive fields were plotted both before and after the external ears were mechanically restrained.

Some recordings were made in the inferior colliculus. The two colliculi were differentiated by electrode placement and the effects of electrical stimulation (28).

Data analysis

Statistical programs were developed to test for effects of varying fixation position and to describe the magnitude of receptive field shifts. The response of a cell to a sensory stimulus was defined as the activity occurring within 500 ms after stimulus onset. This interval does not include saccade-related activity since the fixation light and saccade target overlapped at least 500 ms on all delayed saccade trials. The trial was aborted if an eye movement occurred during this interval. Neural activity related to saccadic movements was measured between the offset of the initial fixation light and target acquisition.

The horizontal extent of the receptive fields was determined by plotting the average number of spikes for stimuli presented at each target position as a function of fixation angle. An unweighted means analysis of variance (ANOVA) for unequal sample size was performed on all data. Generally, the sample size (the number of trials with the same target modality) for each target position and initial fixation direction did not differ by more than two or three trials between the data sets compared. Significant main effects were further analyzed by the unweighted means method using the harmonic mean of the sample size.

The fields generated while the subject viewed each of the three fixation lights were compared by visually defining the boundaries of the linear component of the medial edge of the response field. Points between these extremes were fitted with a line using the least-squares method. The mean separation, in degrees, between these leading edges was determined along with the slopes and intercepts of the lines for each fixation direction.

RESULTS

The effect of varying eye position on responsiveness to auditory stimuli was tested in 121 of 136 sound-sensitive neurons isolated in the SC and in five cells isolated in the inferior colliculus. Acoustically responsive neurons in the SC were located in the deeper layers, below the visual-motor and saccade-related burst cells studied in the preceding paper (15). Most auditory units were found in central and posterior areas of the colliculus, regions representing intermediate and large motor error signals. Of 124 units in the SC tested with both auditory and visual stimuli, all but two were responsive to both types of stimuli. In contrast, 57 of 59 visual-motor cells isolated in the intermediate layers displayed sensory responses to visual but not acoustic stimuli (15).

Effects of eye position on responsiveness to auditory stimuli

The activity of most acoustically responsive neurons isolated in the SC was altered by changes in eye position. Typical data are illustrated in Fig. 2. Single trial data and cumulative histograms of spike activity for a single neuron are shown in Fig. 2*A*. For all trials illustrated in this panel, the speaker was located 20° to the right and elevated 6°. When the subject fixated the left target, each auditory stimulus evoked a vigorous response. When the monkey was fixating the center target or the right target, responses to an identical stimulus presented from the same speaker location were markedly attenuated or completely absent.

The average number of spikes in the auditory response is plotted as a function of horizontal speaker position and as a function of initial fixation direction in Fig. 2*B*. In order to plot a cross section of the receptive field, the speaker was placed ±40° (in 10° increments) from the primary position along the azimuth while maintaining speaker elevation at the optimal position (6° elevation). Stimuli were presented only within the oculomotor range of the subjects since auditory responses habituated rapidly if the animal did not attempt to look to the noise source. Although for the cell illustrated in Fig. 2 the optimal speaker position for each fixation direction could not be ascertained, a distinct shift in the medial boundary of the auditory receptive field occurred when eye position was varied. For example, when the animal was fixating the 24° left target, vigorous responses occurred when auditory stimuli were presented straight ahead and 10° right (Fig. 2*B*). However, these stimuli were not in the cell's receptive field when the center or right fixation targets were used. For data collected from this cell, the main effect of fixation direction was statistically significant ($P < 0.001$); the simple main effect of eye position was significant at the 0.001 level for 10, 20, 30, and 40° rightward targets.

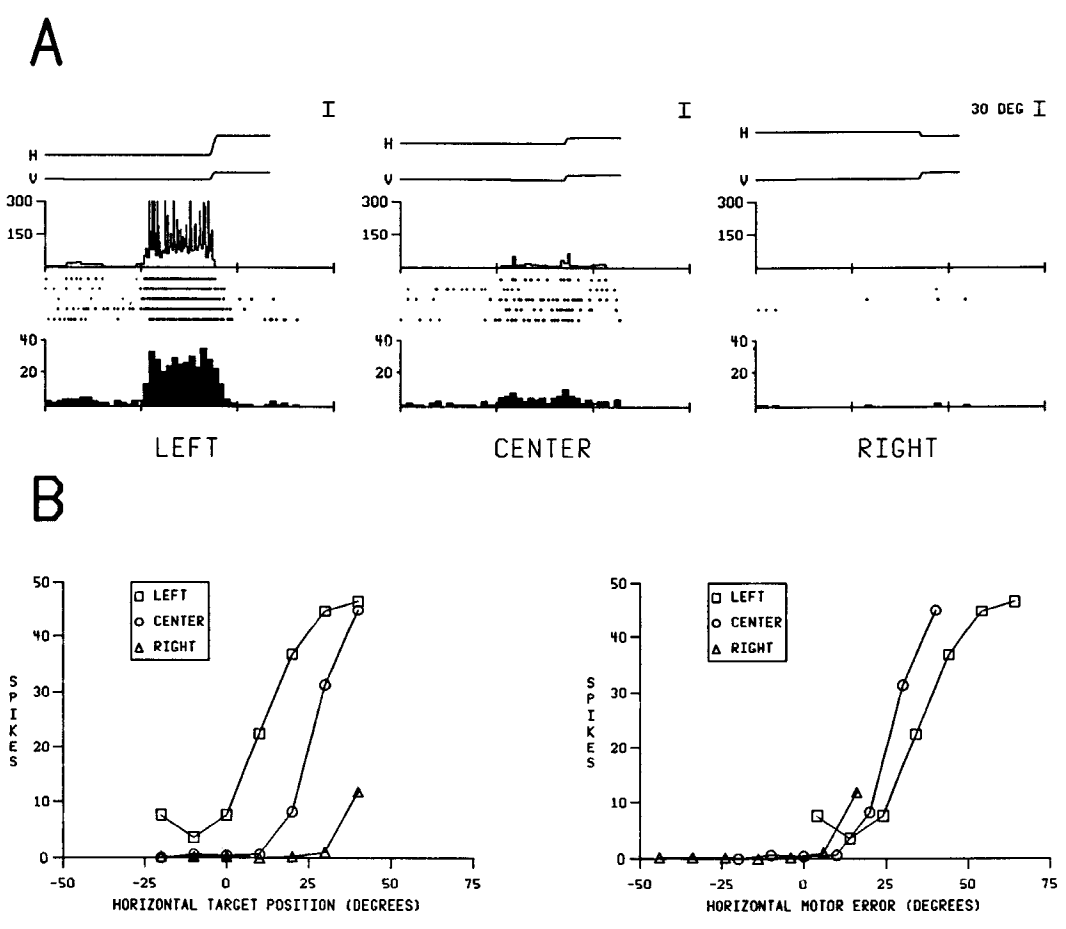

FIG. 2. The shift of auditory receptive fields of a collicular neuron with changes in eye position. *A*: single trial data illustrating the eye position effect. The *top two traces* in each *panel* represent horizontal (H; up, right) and vertical (V; up, up) eye position, respectively, for a single trial. The instantaneous firing rate for the same trial is shown in the third row. Rasters illustrating unit activity for 5 representative trials are shown next. The *bottom trace* is a cumulative histogram of the neural activity for these 5 trials. The time base represents a total of 3 s; target onset occurred at 1 s. For all trials illustrated, the auditory target was kept stationary, relative to the head, at 20° left and 6° up from center. *Left*: the initial fixation direction was 24° left of center. *Center*: the central fixation light was used. *Right*: the initial fixation direction was 24° right of center. *B*: *left*: plots of the number of spikes in the first 500 ms after the onset of the auditory stimulus as a function of the azimuth of the auditory target. Minus, left; plus, right. *Right*: the same data are replotted as a function of horizontal motor error, the horizontal component of the eye movement required to look to the target.

If the receptive fields of auditory cells in the primate SC were encoded in head coordinates, then, in Fig. 2*B* (left), the cross sections of the receptive fields plotted for different fixation positions would be superimposed. But eye position clearly affected the spatial tuning of this cell, resulting in a shift of the auditory receptive field as fixation was varied. In the right panel of Fig. 2*B*, these same data are replotted in motor error coordinates. As in the left panel, the average number of spikes in the first 500 ms after the onset of the auditory stimulus is plotted on the ordinate. The abscissa, in this case, represents the difference in azimuth between the initial fixation direction and the speaker position (horizontal motor error). As can be seen, the data are much better aligned when plotted in motor-error coordinates than when head-centered coordinates are used.

For the cell illustrated in Fig. 2, the firing rate varied with the direction of fixation even before the saccade targets were presented. The

mean number of spikes recorded in a comparable 500-ms prestimulus interval was 8.16 for left fixation, 2.05 for center fixation, and 0.44 for the right fixation condition. This effect of eye position was found to be statistically significant (ANOVA; $P < 0.001$). A significant effect of eye position on firing rate during the fixation interval was found in two other cells; effects were comparable on auditory and visual trials. Thus, some collicular cells carry a signal proportional to eye position, a signal necessary for the conversion of head-centered spatial codes into signals based on motor error (see DISCUSSION).

The activity of another collicular neuron is illustrated in Fig. 3. For the trials shown in Fig. 3*A*, the speaker was 30° left and 8° above center. In the left panel, the initial fixation was 24° left resulting in a motor error of 6° left and 8° up. Data in the middle panel were collected during central fixation; motor error was 30° left and 8° up. Trials shown in the right panel required fixation of the right target and motor error was 54° left and 8° up. This cell was unusual in displaying an initial sensory response and a second burst of activity beginning before the saccade to the sound source. A discussion of this second burst will follow. As illustrated, when identical stimuli were presented from the same location in auditory space, the initial sensory response decreased if eye position was changed from left to center to right. Only the medial border of the receptive field could be plotted when the subject was viewing the left fixation light (Fig. 3*B*, left). With central fixation, the auditory receptive

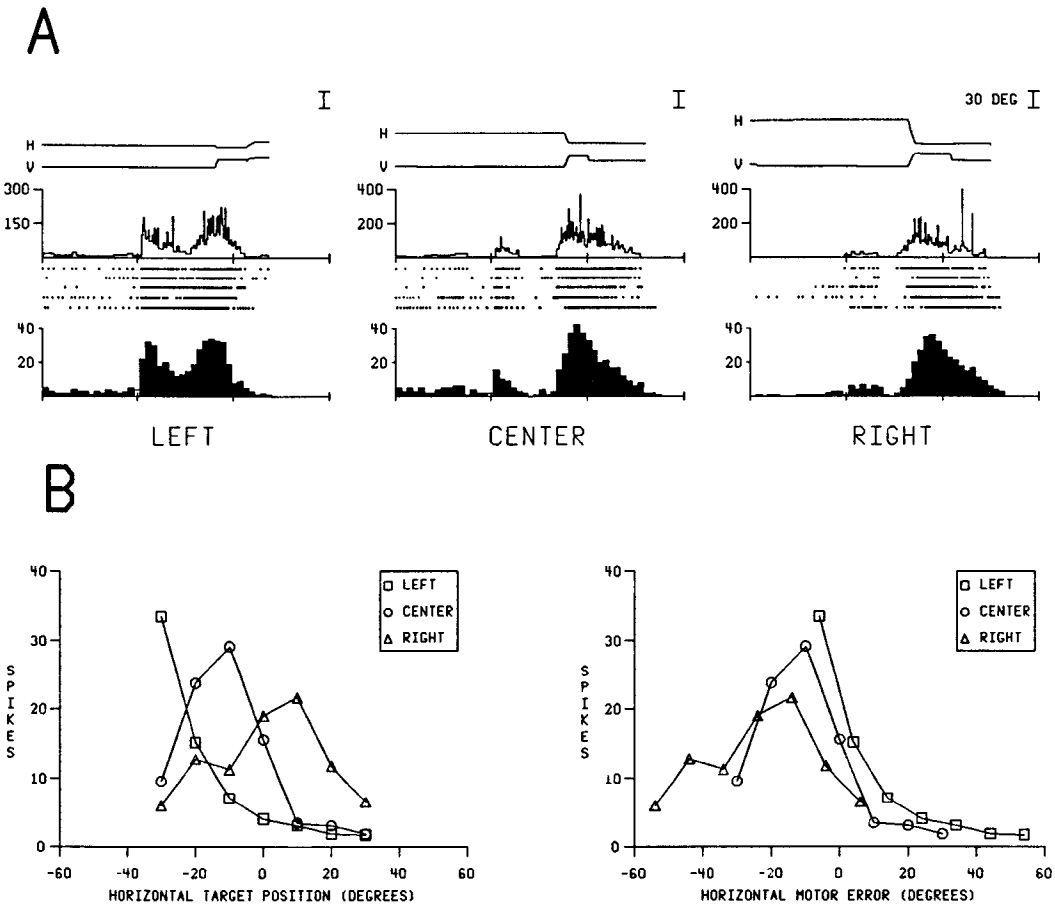

FIG. 3. Effects of eye position on responsiveness to auditory stimuli for a collicular cell displaying an initial sensory response followed by a later motor response. The target was maintained at 30° left and 8° up from center for all data shown in *A*. See Fig. 2 legend and text for details.

field shifted to the right, a lateral border of the receptive field was evident, and the optimal speaker location was 10° left of the primary position. When the animal fixated the right target, the receptive field was further displaced to the right and the optimal speaker location was 10° right of midline. A two-way ANOVA revealed a significant main effect of fixation direction ($P < 0.01$) for this cell. The follow-up test for the simple main effects showed that eye position significantly altered the neural response in six of the seven speaker locations ($P < 0.001$). When these same data are plotted in motor error coordinates (Fig. 3*B*, right), the curves are more closely aligned.

In contrast to the striking effect that eye position had on the acoustic response of neurons in the superior colliculus, changes in eye position did not affect the response of any of the five neurons isolated in the inferior colliculus. Single trial data and cumulative histograms for a representative cell are illustrated in Fig. 4*A*. For the trials shown, the speaker was on the median plane and 4° above center. Changes in the initial fixation direction did not affect the pattern of neuronal firing. The left panel shows data obtained with leftward fixation. Data obtained with central fixation are illustrated in the center panel and the right panel illustrates data collected when the right fixation light was employed. A horizontal cross section of the receptive field of the cell is shown in Fig. 4*B*. The plots for the three fixation directions are almost perfectly superimposed. This is what would be expected for a cell that coded the position of a sound source relative to the head without regard to the trajectory of the eye movement required to look toward the sound source. Eye position had no statistically significant effect on the response of this cell to auditory stimuli ($P > 0.25$).

Eye position, or the direction of fixation while saccade targets were presented, significantly altered the sound-induced responses in 99 of the 121 SC cells tested ($P < 0.05$). Many of the remaining 22 cells also seemed to display an eye position effect; but with the limited number of trials obtained, the effect did not reach statistical significance. The main effect of eye position was significant at the 0.001 level in 72 of these SC cells. In contrast, no significant effect of eye position was observed for any of the five inferior colliculus cells examined.

Dissociating sensory and motor responses

The purpose of training subjects on the probe trial task was to eliminate movement-related influences by testing the responses of neurons to auditory stimuli in the absence of saccadic eye movements. However, an off-line analysis of data collected during probe trials revealed that at the end of the trial animals usually looked toward the remembered position of the sound source even though reinforcement had already occurred. Figure 5 presents data obtained on probe trials from the same cell illustrated in Fig. 2. In Fig. 5*A*, single trial data are shown for trials in which the speaker was positioned 30° right of center and elevated 6°. For the trials shown, at the end of the trial the monkey eventually made a saccade in the general direction of the speaker. But saccades on probe trials occurred at least 500 ms later than saccades on delayed saccade trials (Fig. 2). On delayed-saccade trials, the auditory-evoked activity was maintained at a fairly steady rate until the saccade to the speaker location was initiated (see Fig. 2). On probe trials, this tonic activity decreased markedly when the speaker was turned off, ~800–900 ms after the target was first presented. The cells then displayed a second burst of activity preceding the eye movement toward the (now silent) sound source. This effect is seen prominently in the single trial data collected when the center fixation light was used (Fig. 5*A*, center panel). During these trials, the cell was quiescent for ~200 ms between the end of the initial tonic activity and the presaccadic burst. Note that this cell exhibited a small saccade-related response even when the monkey made leftward eye movements, as seen with the trials initiated from the right fixation point (Fig. 5*A*, right panel).

In Fig. 5*B*, the number of spikes in the 500 ms following the onset of the auditory stimulus is plotted as a function of horizontal target position and as a function of horizontal motor error. Just as found during delayed-saccade trials, the main effect of eye position was significant with probe trials ($P < 0.001$) and the receptive fields were better aligned when plotted in motor-error coordinates. Similar results were found for five other cells studied under similar conditions. The maximum average number of spikes was approximately the same for probe and delayed-saccade trials for this cell. For other cells analyzed in this manner,

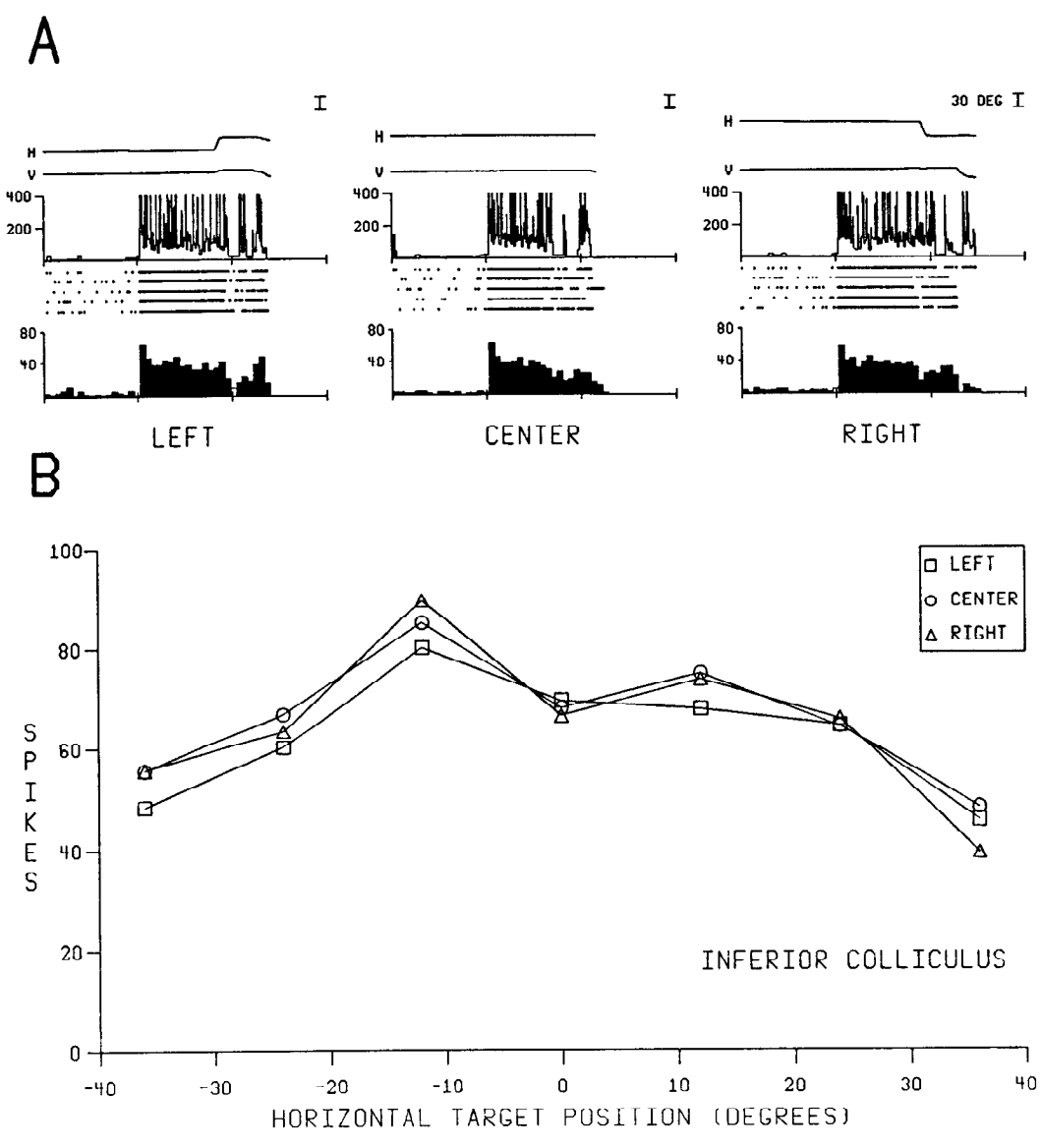

FIG. 4. *A*: single trial data obtained from a cell isolated in the inferior colliculus. The speaker was at the midline and elevated 4° for all trials. *B*: plots of the number of spikes in the first 500 ms after target onset as a function of target azimuth and fixation direction. Unlike cells in the superior colliculus, variations in fixation position did not affect the responses of cells in the inferior colliculus.

the number of spikes occurring on probe trials was reduced, reflecting the habituation of responses.

Field shift variations

If the responses of auditory cells were coding motor error, then the shift in the receptive field should be of the same magnitude as the change in fixation position. Yet while the fixation lights were separated by 24°, for some cells the shift in the receptive fields was smaller than 24°. A typical example of a cell with a smaller receptive field shift is illustrated in Fig. 6*A*. Eye position was statistically significant ($P < 0.001$) but the fields were only separated by ~8 and therefore compensated for only ~34% of the change in eye position. Nor are these data aligned when plotted as a function

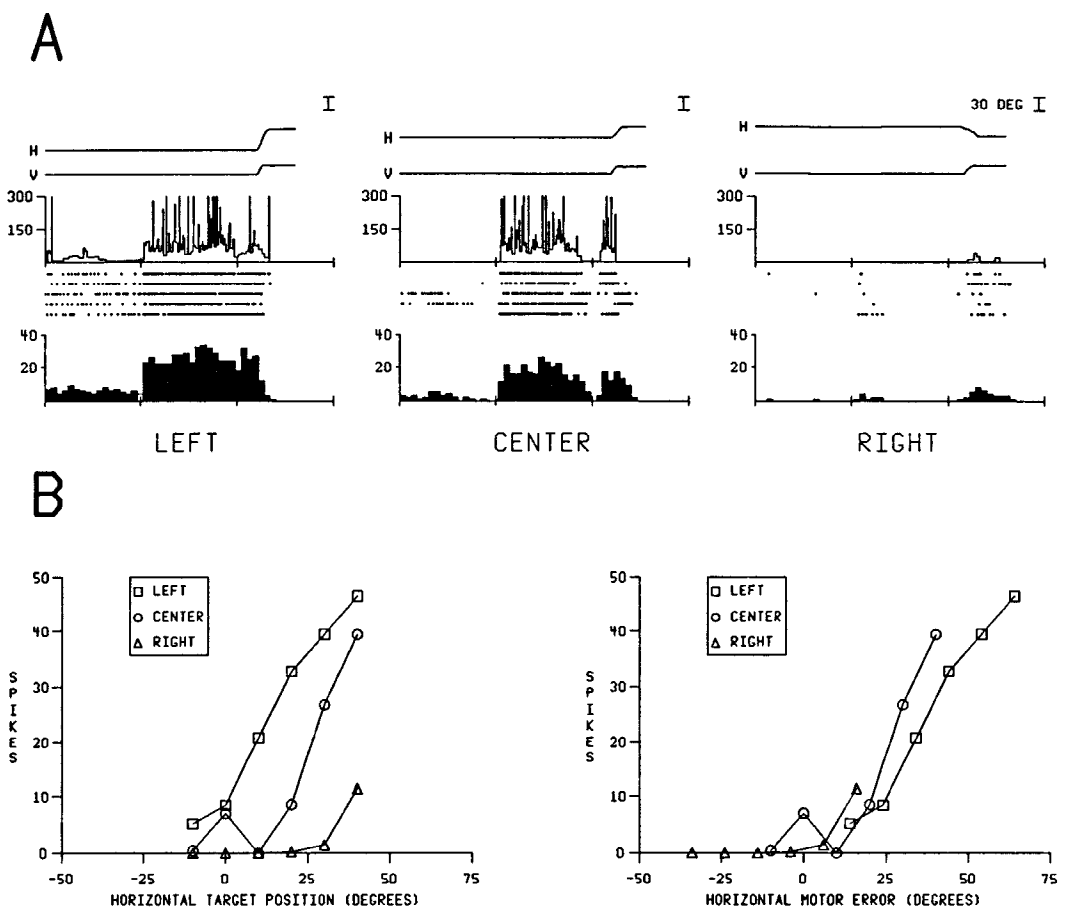

FIG. 5. *A*: single trial data collected during probe trials. The speaker was located 30° right and elevated 6° in all cases. *B*: plots of the magnitude of the neural response as a function of target azimuth and fixation direction. See text for further details.

of motor error (Fig. 6*B*), defined as the difference between fixation position and speaker position. However, on most auditory trials the animal's response consisted of more than 1 saccade and even after multiple movements a discrepancy or error existed between the subject's direction of gaze and the actual speaker location. Thus these data were replotted as a function of the average horizontal direction of gaze at the end of the first movement (Fig. 6*C*) and as a function of the average change in horizontal position (actual horizontal motor error) in Fig. 6*D*. If the discharge of this cell is related to the actual position of the speaker in space, the curves in Fig. 6*A* should be aligned. If the cell's activity is related to the position in space to which gaze is directed after the first movement, then the curves in Fig. 6*C* should be aligned. Finally, if the cell's activity is related to actual horizontal motor error, the difference between the fixation position and the actual movement that occurred, then the curves in Fig. 6*D* should be aligned. As can be seen, the activity of this cell appears to represent a signal midway between motor error and head reference systems.

Quantitative analysis of field shifts

An index of the magnitude of the receptive field shift was obtained for each cell. By visual inspection, the linear portion of the medial border of each of the three fields was determined. These points were then used to obtain a least-squares regression line for each fixation direction. The mean separation of these three lines was calculated at a point 50% between

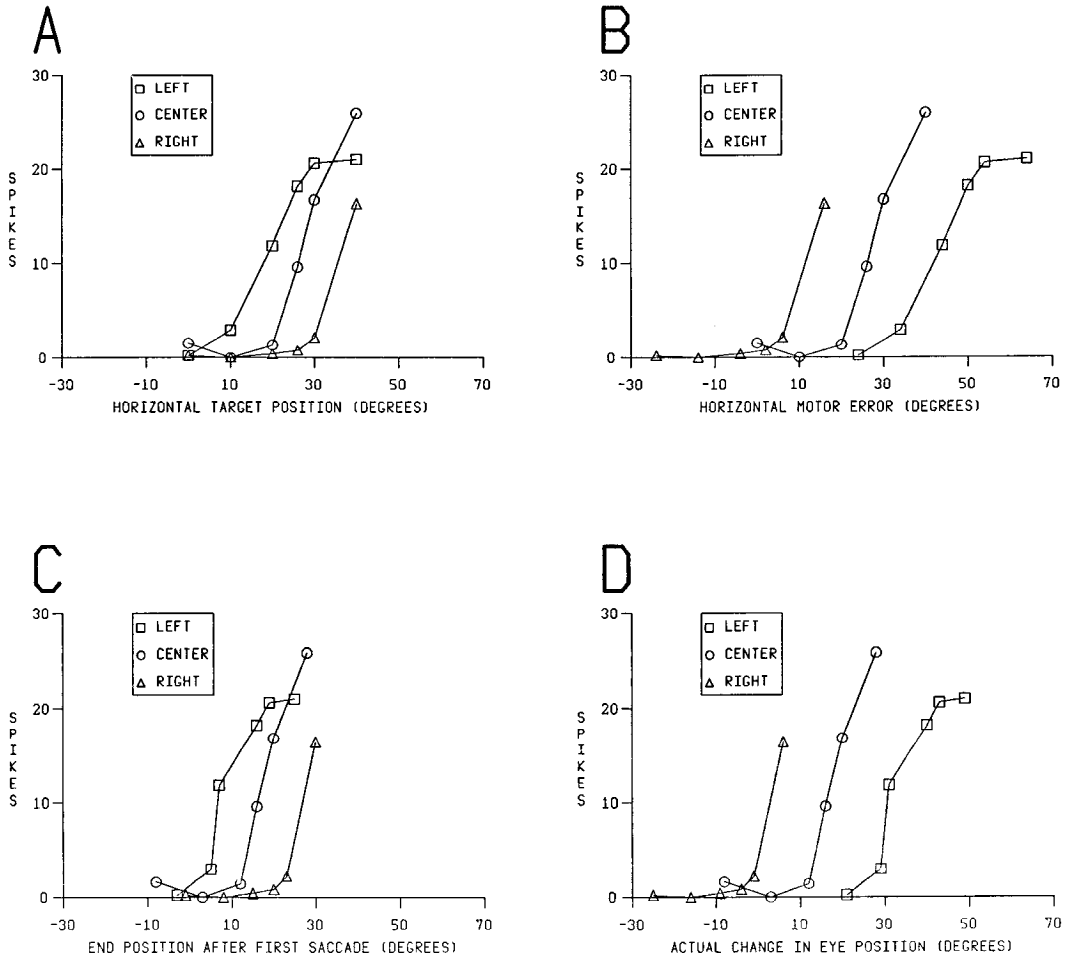

FIG. 6. Example of a cell in which the receptive field shift was less that the change in eye position. *A*: plot in head coordinates. *B*: plot in horizontal motor-error coordinates. Horizontal motor error defined as the difference between horizontal fixation position and horizontal target position. *C*: plot of response magnitude as a function of the average gaze position at the end of the first saccade to each speaker location. *D*: plot of response magnitude as a function of horizontal motor error. Horizontal motor error defined as the average change in horizontal eye position for the first saccade to each target.

the minimum and maximum number of spikes. This number served as an index of the magnitude of the receptive field shift with changes in eye position.

An example of this analysis procedure is illustrated in Fig. 7 for one cell. The medial boundaries of the receptive fields are plotted in head coordinates in Fig. 7*A*. The linear range for the left fixation field was judged to be from midline to 20° right; this range extended from 10 to 40° right for central fixation and from 20 to 40° right with fixation of the right target. The least-squares analysis of these data points is shown in Fig. 7*B*. The mean separation between these three lines was 10.7°.

A histogram representing the receptive field shifts for the entire population of auditory and visual cells is shown in Fig. 8. A unimodal distribution was obtained for both the auditory (above) and the visual fields (below). The average shift of the auditory receptive fields for a 24° change in fixation was 12.9° (SD, 7.01). For visual fields analyzed in the same manner, the mean value was 21.7° (SD, 8.59). The range for the visual data was from 5.5 to 46° and from 0.2 to 34.7° for the auditory data.

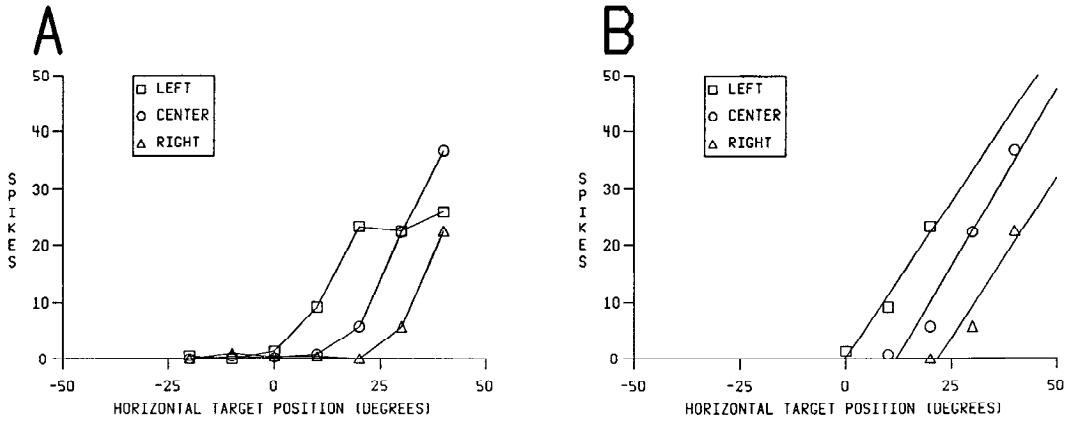

FIG. 7. Quantitative analysis of the magnitude of receptive field shifts. *A*: plots of horizontal extent of auditory receptive field for a cell in the left superior colliculus. *B*: least-squares fit of the data points along the medial edge of the receptive field.

The null hypothesis that the means of the two samples did not differ was rejected at the 0.001 confidence level.

Horizontal and vertical tuning of auditory and visual receptive fields

Our results confirm previous reports (5, 7, 8, 19, 33–35) that the response magnitude of visually responsive collicular neurons is a function of stimulus location within the receptive field. The maximal response occurs when stimuli are presented at the center of the receptive field and the response progressively decreases as stimuli are presented further away from the receptive field center. In our experiments, the horizontal position of the visual stimulus within the receptive field had a statistically significant effect for 41 of the 42 cells tested (ANOVA; $P < 0.05$). Similarly, for three of the four cells studied, the vertical position of the visual target within the receptive field significantly affected neuronal responses ($P < 0.05$). For 75 of 81 cells studied with auditory stimuli, variations in the horizontal position

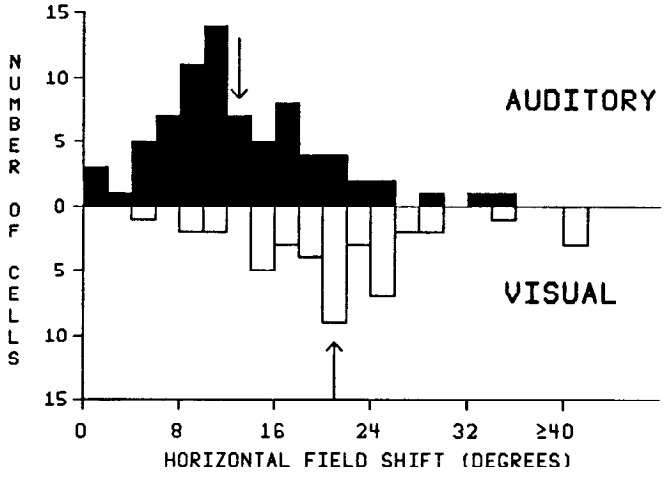

FIG. 8. Distribution of receptive field shifts. *Top*: the average separation (*vertical arrow*) for auditory receptive fields was 12.9° for 24° changes in eye position. *Bottom*: the average separation (*vertical arrow*) for visual receptive fields was 21.7°.

of the sound source significantly ($P < 0.05$) altered the neuronal responses. However, only three of seven cells tested displayed significant variations in response when the elevation of the auditory stimulus was varied.

While the responses of cells to variations in the elevation of auditory stimuli were studied in only a few cells, the difference between horizontal and vertical tuning was striking. A horizontal cross section of the auditory receptive field is plotted for one cell in Fig. 9*A*. Speaker elevation remained constant (8° above horizontal). In Fig. 9*B* the horizontal position of the speaker was maintained at 20° left while elevation was varied from 30° below to 30° above horizontal. For variations in azimuth, the main effect of speaker position was significant ($P < 0.001$). No significant effects of varying speaker elevation were obtained ($P > 0.05$). The auditory receptive field of this cell and most of the other units studied was essentially unrestricted in elevation but tuned along the azimuth.

For auditory responses, the interaction between horizontal speaker position and fixation direction was statistically significant in 69% of the cells studied. Significant interactions between speaker elevation and fixation direction were observed in only one of seven cells studied ($P < 0.05$). For visual responses, 86% of the cells tested with variations in the azimuth of visual stimuli and two of four cells tested with variations in stimulus elevation displayed significant interaction effects between the position of the visual stimulus and fixation direction. Significant interaction effects were not observed for any of the auditory fields of cells in the inferior colliculus.

The role of pinna movements

Systematic variations in the position of the pinnae associated with the different fixation positions could affect plots of the auditory receptive fields. The subjects used in this study (*Macaca mulatta*) are able to produce large pinna movements. Usually these consisted of transient movements toward unexpected sounds, and we never observed subjects orienting their pinnae in a single direction for extensive periods of time.

In order to control for the effects of ear movements, the pinnae were mechanically restrained in the resting position prior to recording from 22 cells. In every case except one, statistically significant eye position effects seen with the ears free were also obtained when the external ears were mechanically restrained. Of five cells tested only with the pinnae stationary, all showed a significant fixation effect ($P < 0.001$).

An example of these data is shown in Fig. 10. First, the receptive fields were plotted with the external ears mechanically restrained (Fig. 10*B*). Then, the receptive fields were replotted after the ears were released (Fig. 10*A*). In both cases, the main effect of fixation position was significant ($P < 0.001$). The elevation of the speaker during all trials used to generate this figure was 8° below horizontal. Although minor differences are noticeable between the

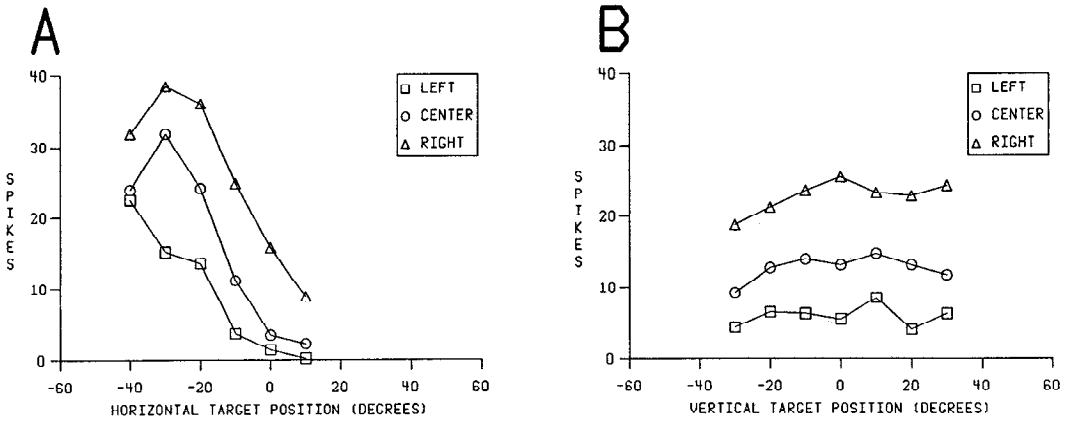

FIG. 9. Horizontal vs. vertical tuning of auditory receptive fields. *A*: tuning in the horizontal plane for a typical collicular cell. *B*: tuning in the vertical plane for the same cell.

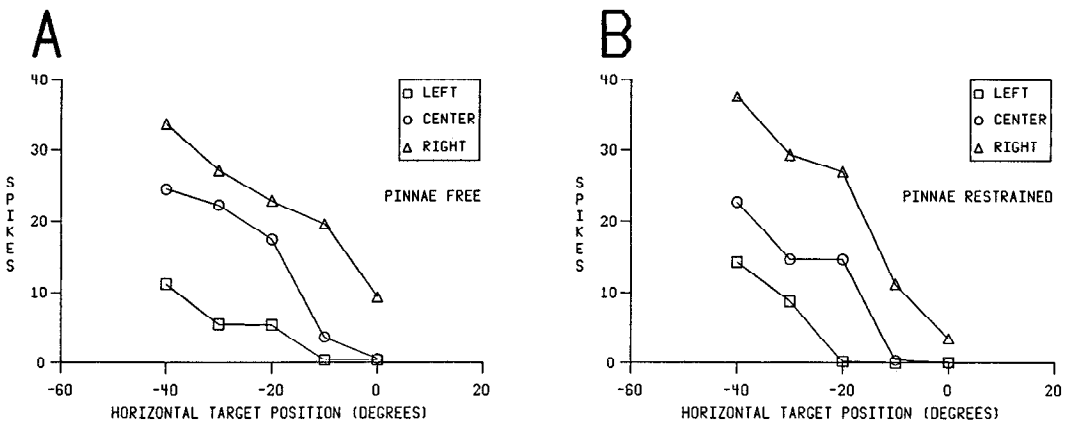

FIG. 10. The effects of restricting pinna movement on auditory receptive fields. *A*: auditory fields plotted with the external ears free. *B*: data from the same cell collected while the pinnae were mechanically restrained.

plots, it is clear that stabilizing the external ears did not eliminate the eye position effect.

Further comparisons of auditory and visual responses

The intensity of the auditory and visual stimuli was not systematically varied in the present experiment and no attempt was made to obtain "subjective" matches for the auditory and visual stimuli along the intensity dimension. Instead, suprathreshold stimuli were used and stimulus intensity was held constant throughout the experiment. For the stimulus parameters used, we observed differences in the latency of neural responses to auditory and visual stimuli, differences in the relative sensitivity of individual neurons to auditory and visual stimuli, and, for the same cell, differences in the sharpness of tuning of auditory and visual receptive fields.

For 87% of the 122 cells tested that were responsive to both auditory and visual stimuli, the response latency was shorter for auditory than for visual stimuli. About 4% of the cells had equal latencies for stimuli of both modalities, and 9% of the cells displayed shorter latencies when visual stimuli were presented. Figure 11 presents a histogram of the distri-

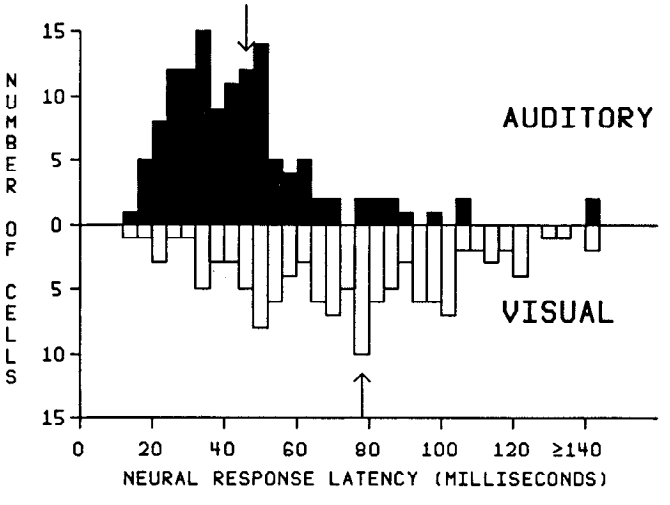

FIG. 11. Distribution of response latencies of collicular cells for auditory and visual stimuli. *Top*: distribution of latencies of sound-induced activity. Mean, 44.8 ms. *Bottom*: distribution of latencies of visually induced activity. Mean, 76.1 ms.

bution of response latencies using the optimal stimulus location and fixation direction for both unimodal and bimodal collicular cells. The mean response latency for sound-induced responses was significantly ($P < 0.001$) lower (44.8 ms; SD, 22.77) than the average latency on visual trials (76.15; SD, 33.58). The mean latency for sound-induced responses in the inferior colliculus was 28 ms.

For 35% of the bimodal cells encountered, the magnitude of the neural response was greater for auditory trials than for visual trials. With another 36%, the response at the optimal target position for each modality was approximately the same. The remaining 29% appeared to be more sensitive to visual stimuli than auditory ones. The relative sensitivity of single cells to auditory and visual stimuli may vary depending on stimulus parameters. It is unlikely that the white-noise bursts used were the optimal auditory stimuli for all cells studied. What these data indicate is that for the constant auditory and visual stimuli used in these experiments, collicular cells display differential sensitivity to auditory and visual stimuli.

The least-squares analysis of the medial border of the receptive field (see Fig. 7) allowed a comparison of the relative sharpness of spatial tuning of auditory and visual receptive fields. For 42% of the sample, the slopes of the best fit lines for auditory fields were higher (sharper tuning) than for the visual fields. Another 53% showed the opposite relationship: visual receptive fields were more sharply tuned than auditory receptive fields. The remaining 5% of the sample had about the same degree of tuning for both modalities. Since spatial tuning may become sharper if optimal stimuli are used, these proportions may vary with other combinations of auditory and visual stimuli.

Comparison of first and second bursts

Although most cells (71%) displayed a tonic increase in activity that was maintained until just after the eye movement or stimulus offset, some units (29%) were clearly biphasic (see Fig. 3*A*). For several biphasic cells, varying eye position differentially affected the first and second bursts. An example is shown in Fig. 12. The number of spikes in the first (sensory) burst is plotted as a function of fixation position and horizontal target position in Fig. 12*A*. The number of spikes in the second burst for the same trials is plotted in Fig. 12*B*. When the first burst is plotted for auditory trials, just the medial border can be visualized when the left fixation light is employed, but both the medial and lateral borders are evident during the other two fixation conditions. In contrast, the plot of the second burst (Fig. 12) just shows the medial edges. Although it is tempting to define the first burst as one based on motor error and the second as head-centered, the position of the eyes in the orbit was significant for both the second ($P < 0.001$) and the first bursts ($P < 0.01$).

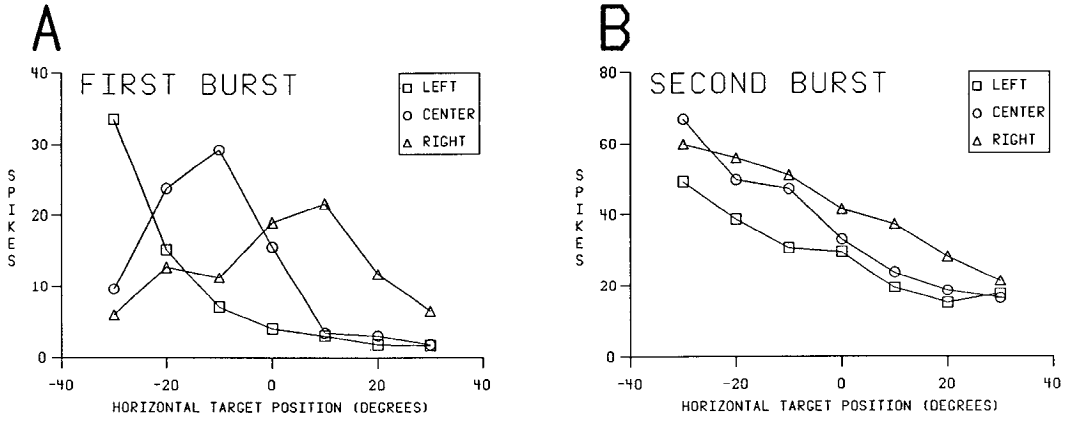

FIG. 12. Comparison of plots of initial sensory response (*A*) and subsequent burst (*B*) for a single cell. See text for further details.

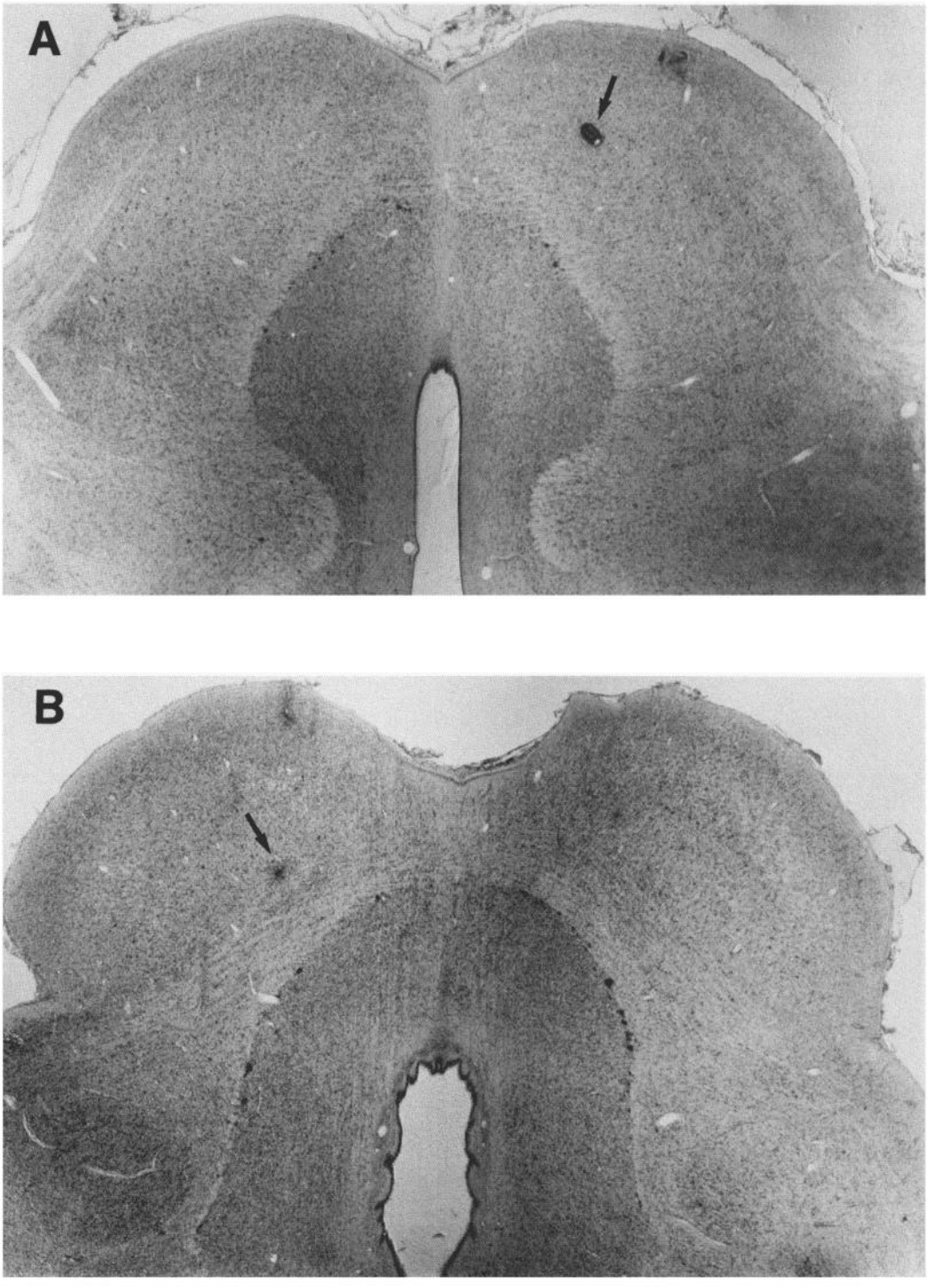

FIG. 13. Lesions (indicated by *arrows*) made at sites where auditory cells were isolated in *monkey A* (*top*) and *monkey B* (*bottom*).

Histological reconstruction of recording sites

The locations of lesion sites where auditory cells were encountered in *monkeys A* and *B* are shown in Fig. 13. Compare these ventrally located recording sites with those marking premotor cells, in these same animals, shown in Fig. 8 of the preceding paper. For both auditory cells, the effect of eye position on the neural response to sounds was statistically significant. The receptive field plots from both units were separated by ~10° for every change in fixation direction. Microstimulation (10 μA) at the site illustrated in the upper panel resulted in a 26° right, 14° upward movement. The threshold for electrical stimulation was 35–40 μA for the auditory cell marked in the lower panel, and the movement produced was 10° right, 8° up.

DISCUSSION

The effect of eye position on responsiveness to auditory stimuli

The deeper layers of the SC are a site where visual, auditory, and somatosensory signals converge as well as an area containing neurons with motor properties. Based on the findings of the previous paper (15), auditory and visual signals have been translated into common coordinates at the level of the SC and share a pathway for the generation of saccadic eye movements. It is not known, however, whether the translation of sensory signals into motor coordinates occurs prior to or within the SC. Nor is it known in what coordinates auditory signals observed in the SC are encoded. The present experiment focused on the question of the frame of reference of auditory signals found in the deeper layers of the colliculus. Two mutually exclusive hypotheses were tested. The first was that auditory signals in the colliculus are encoded in head coordinates. If this hypothesis is correct, then, with the head fixed, the response of auditory neurons depends entirely on the location of the speaker and should not be affected by variations in eye position. The second hypothesis states that the responses of auditory cells in the SC specify the trajectory of the movement required to look to an auditory stimulus. If this hypothesis is correct, the responses of collicular neurons to acoustic stimuli should depend on both the position of the speaker in space and the position of the eyes in the orbits.

Experimental results support the second hypothesis. The response to auditory stimuli was significantly affected by variations in eye position for 99 of the 121 collicular cells tested. For each initial fixation position, the location of the auditory stimulus that would evoke a maximal response was predictable. Targets requiring a movement of a particular direction and amplitude, rather than targets located in a particular part of auditory space, were maximally effective.

Our conclusions are exactly the opposite of those reached by Harris, Blakemore, and Donaghy (13). In their experiments, an alert, untrained cat was placed in a darkened room with the head fixed. Auditory stimuli were presented at various locations while other sounds elicited changes in gaze. The neural responses were averaged for eye positions in three ranges: within 7° of midline, greater than 7° right, and greater than 7° left of center. Of the three cells tested quantitatively, no changes in the neural response to sounds were noted with variations in eye position. While the functional properties of neurons in the cat colliculus may differ from those of the monkey, the conclusion that the position of the eyes in the orbits does not affect the response of neurons in the cat SC to auditory stimuli is unwarranted. In addition to the problem of generalizing from such a small sample, averaging data for the different eye positions may have obscured an effect. Also, if neurons in the cat SC are like those in the monkey, responses habituate quickly if the sound source is not also the target for an orienting movement. The conditions of the experiment conducted by Harris and colleagues were optimal for the occurrence of rapid habituation. A more controlled and exhaustive study should be undertaken before it is concluded that the responses of auditory neurons in the cat differ from those observed in this experiment.

CONTROLS FOR CONFOUNDING VARIABLES. A number of variables, other than eye position, that might account for these results were considered. Although the experiments were not conducted in an anechoic chamber, and the restraint chair and apparatus for generating the magnetic fields could produce variations in reflection patterns when stimuli were projected from different speaker locations, it is unlikely that these contaminations of the acoustical signals can account for our major

findings. First, the distortions were not severe since, based on measures of the direction and amplitude of saccades to the acoustic stimuli, the animals were able to localize the stimuli with reasonable accuracy. Second, the major effect on the response of auditory neurons was produced by changing the position of the eye in the orbit, not by manipulating the frequency, intensity, or location of the auditory stimulus. Any acoustical distortions produced by the uncontrolled auditory environment would be identical for stimuli presented with the speaker at a particular azimuth and elevation and, therefore, could not account for differential neural responses occurring with variations in eye position.

Some neurons in the auditory cortex (25) and inferior colliculus (2, 30) of the cat have receptive fields that are aligned with the acoustic axis of the contralateral pinna. This implies that when the ears are oriented in different directions, the spatial location of the auditory receptive field of a particular cell changes. Thus systematic variations in the position of the pinnae associated with different fixation positions could produce misleading results. If, for example, the external ears were rotated to the right when the animal fixated the right target, then a sound source would also have to be moved to the right to duplicate the interaural time and intensity differences present when the pinnae were directed straight ahead. To control for this confounding variable the pinnae were mechanically restrained while fixation position was varied. The responses of neurons in the superior colliculus to auditory stimuli depended on the position of the eyes in the orbits, even when the external ears were held stationary. It should also be noted that if stereotyped movements of the pinnae associated with different fixation positions account for the results obtained from recordings of neurons in the SC, then similar results should be obtained when recording from neurons in other brain structures. This was not the case. The responses of neurons isolated in the inferior colliculus were not affected by changes in eye position.

Also of concern was the possibility that the neural activity in question was merely premotor activity and not actual responses to an auditory stimulus. Like visually responsive quasi-visual cells found in the intermediate layers of the SC (22), most neurons described in this paper cannot be classified as either strictly sensory or purely motor. Rather they exhibit both qualities. Like pure sensory neurons, these cells produce responses tightly coupled to stimulus onset, rather than to movement onset. On both delayed-saccade and probe trials in which the interval between the onset of the noise stimulus and the onset of a saccade toward the target was quite variable, the neural response was always linked to stimulus onset, not response onset. Additional evidence that these neurons have sensory properties is derived from a consideration of their bimodal responses. Most auditory cells could be activated by either auditory or visual stimuli, but the vigor of the neural response depended on target modality, even on those trials in which identical motor responses occurred. Some cells discharged more vigorously to auditory stimuli, others to visual targets. If the neural response were merely a premotor event, then the response should be the same for comparable movements mediated by auditory and visual targets. Yet, the response of these cells is not purely sensory since it depends on the trajectory of the movement required to look to the stimulus.

MAGNITUDE OF RECEPTIVE FIELD SHIFTS. If the responses of auditory cells are coding motor error, then the shift in the receptive field should be the same as the change in fixation position. But in our analysis, the average magnitude of the auditory receptive field shift was 12.9°, ranging from 0.2 to 34.7°. We have considered three possible explanations for the failure of the receptive field to shift by the same amount as the change in fixation position. The first is that the differences are due to lack of precision in the definition of receptive field boundaries and/or other measurement errors. Since targets were presented only within the oculomotor range, the optimal target location for each cell at each fixation point could not always be determined. As a result, the magnitude of the field shifts with changes in eye position was estimated from the separation of the linear portion of the medial edges of the receptive field border. These edges were not always parallel and the arbitrary assignment of differences at the 50% point may have introduced errors. It is unlikely, however, that the errors introduced in this manner would account for a large percentage of the observed variance or would produce, on average, an error of 13°. The second possibility is that there

is a gradual transition, within the SC, from sensory signals in head coordinates to signals in motor error coordinates. In this case, cells with different amounts of receptive field shift would represent different points in this process. The third possibility is that the incomplete receptive field shifts are due to a failure to take into consideration the vertical component of motor error. In those cases in which the receptive field or movement field of collicular neurons has been examined in detail, the response fields are graded. For example, the number of spikes in the burst of a saccade-related burst cell will decrease if the movement differs from the optimal saccade in either direction or amplitude (31, 32). Thus, in our experiment while auditory and visual stimuli were presented at the same spatial location, there were differences (idiosyncratic for each animal) in the trajectory of the initial saccade to auditory and visual targets. We attempted to take this into account by plotting response magnitude as a function of actual horizontal motor error, but were unable to control for differences in the vertical component of the initial saccade. What is needed are complete plots of the response fields of auditory neurons. Then it would be possible to see if there is a correspondence between *1*) unit activity on single trials, *2*) "perceived" motor error (the trajectory of the actual movement on that trial), and *3*) the three-dimensional profile of the response field of the cell. It is not possible, using the data collected in this experiment, to determine which, if any, of these explanations is most likely to account for the observed results. Additional experiments in which the receptive fields of auditory cells are plotted in more detail are needed.

LOCUS AND MECHANISM OF RECEPTIVE FIELD SHIFT. The statement that the receptive fields of auditory neurons shift is a descriptive one summarizing the finding that the region of auditory space to which individual collicular cells are responsive depends on the position of the eye in the orbit. Neither the locus nor mechanism for the observed alterations in sensitivity are known. Ultimately, each point in auditory space must be mapped to neurons in all regions of both left and right colliculi. This is necessary since an auditory stimulus at any location can evoke a saccade of any direction and amplitude, depending on eye position at stimulus onset. Thus, with respect to mechanism, one possibility is that each acoustically responsive cell receives inputs from all regions of auditory space and, depending on eye position, inputs from some parts of space are inhibited, whereas those from other regions are facilitated. An alternative method for producing receptive field shifts might involve discrete switching of inputs to collicular neurons from cells responsive to particular zones of the external environment. Based on our data, we have no way of determining which, if either, of these mechanisms might be responsible for alterations in responsiveness occurring when eye position is varied.

The transformation of auditory signals in a head-centered frame of reference into signals of saccadic motor error requires a precise signal of the position of the eyes in the orbits. Potential sources of an eye position signal include both proprioceptive and corollary discharge inputs. In the cat, responses to stretch (6, 29) or electrical stimulation (1) of the extraocular muscles have been recorded in the SC, verifying a proprioceptive projection. Signals proportional to eye position have been found in the frontal eye fields (4), which send a strong ipsilateral projection to the SC (10, 21). Another potential source for an eye position signal is one originating in the nucleus prepositus hypoglossi (23) and traveling via the parabigeminal nucleus (3) to the SC (12). Other areas where eye position signals have been identified include the cerebellar vermis (26), medial vestibular nucleus (24), abducens internuclear neurons (14), oculomotor nucleus (9), and the paramedian pontine reticular formation (18).

Prior to the three cells found in this study, we have never observed neurons in the monkey SC that discharge with rates proportional to eye position. But, since an eye position signal is present in the SC, the transformation of head-centered signals into motor error signals could occur within the SC. At this time, however, the locus for such a transform is not known.

Other findings

HORIZONTAL AND VERTICAL TUNING OF AUDITORY RECEPTIVE FIELDS. An unexpected finding was the failure to find for most cells significant tuning of the receptive fields when target elevation was varied. This was particularly surprising in light of the finding that the accuracy of saccades to auditory targets along

the vertical axis was comparable to that found for targets presented along the azimuth (Jay and Sparks, in preparation). Since we studied only a few cells while target elevation was systematically varied, additional recordings are needed to verify this observation.

LATENCY OF AUDITORY AND VISUAL RESPONSES. For our entire sample, the mean latency of auditory responses was 31 ms shorter than the latency of visual responses. Based on differences in peripheral transduction times of the retina and cochlea, this result is not unexpected. However, the latencies obtained are longer than those reported for neurons in the SC of anesthetized cat and barn owl. In these animals, neural responses to auditory stimuli were observed with latencies of 8–10 ms. Since the auditory stimuli used in our study were well above threshold, these large differences in response latency are probably not due to intensity differences. Another possibility is that short-latency auditory responses were suppressed by the behavioral requirements of the tasks. Whether or not these differences in latency are a species effect or due to other factors could be determined by measuring latencies of auditory responses of collicular neurons in anesthetized rhesus monkeys.

SECOND BURST. A few cells responsive to auditory stimuli also displayed a clear second burst of activity associated with the saccade to the auditory target. The activity of these cells differed in a number of ways from those described in the previous paper (15). The burst of activity had a relatively low instantaneous frequency, lacked a sharp onset and the cells were responsive to auditory stimuli. Neurons described in the previous paper displayed a high-frequency burst of activity with a sharp onset. Most were not responsive to auditory stimuli. For some of the cells described in this paper, responses appeared to be in a head frame of reference although even for these cells, the effects of varying eye position was significant. The possibility that the second burst of these neurons is related to activity of neck muscles and/or attempted movement of the head warrants further study.

Implications for sensorimotor integration

Results of these and other experiments can best be explained by assuming that the intermediate and deeper layers of the primate SC are organized in motor error coordinates. Motor error, the change in eye position required to look to a target, is encoded anatomically since it is the site of activity within the colliculus that specifies saccade direction and amplitude. This imposes constraints on the transformation of sensory signals to be used for directing saccades. Inputs to the SC must specify, by activating a particular subset of neurons, the change in eye position required to look to a target rather than the position of the target in space. This requires a dynamic map of auditory activity within the SC. With each change in eye position, the site of acoustically induced activity shifts to a new location: a location that specifies the metrics of the movement that would direct gaze to the target location.

The dynamic mapping of auditory activity in the SC is illustrated in Fig. 14. When the eyes are directed to the left of a sound source, auditory cells in the left colliculus are active and encode the trajectory of the rightward movement needed for target acquisition. If the viewing axis is shifted to the right of the stationary sound source, neurons in the left colliculus become quiescent and the site of activity induced by the auditory stimulus shifts to the right colliculus. The new location of active neurons codes the metrics of the leftward movement now required to look to the target. Since the visually induced activity of QV cells also forms a dynamic map of motor error (22), visually induced and acoustically induced neural activity in the deeper layers of the SC remain aligned, even when a disparity is introduced between head coordinates and retinocentric coordinates. Although the appropriate experiments have not yet been conducted to determine if activity evoked by somatosensory stimuli is also represented in motor error coordinates, it would not be surprising to discover that the activity of collicular neurons depends on the movement required to look to a tactile stimulus. If so, in the alert animal, responses to tactile stimuli would depend on head position, the position of the eyes in the orbits, the site of stimulation on the body surface, and the angles of intervening joints.

The deeper layers of the SC contain separate representations of auditory, somatosensory, and visual space as well as a map of motor (saccadic eye movement) space. In acute experiments, the sensory and motor maps appear to be aligned and it is commonly assumed that

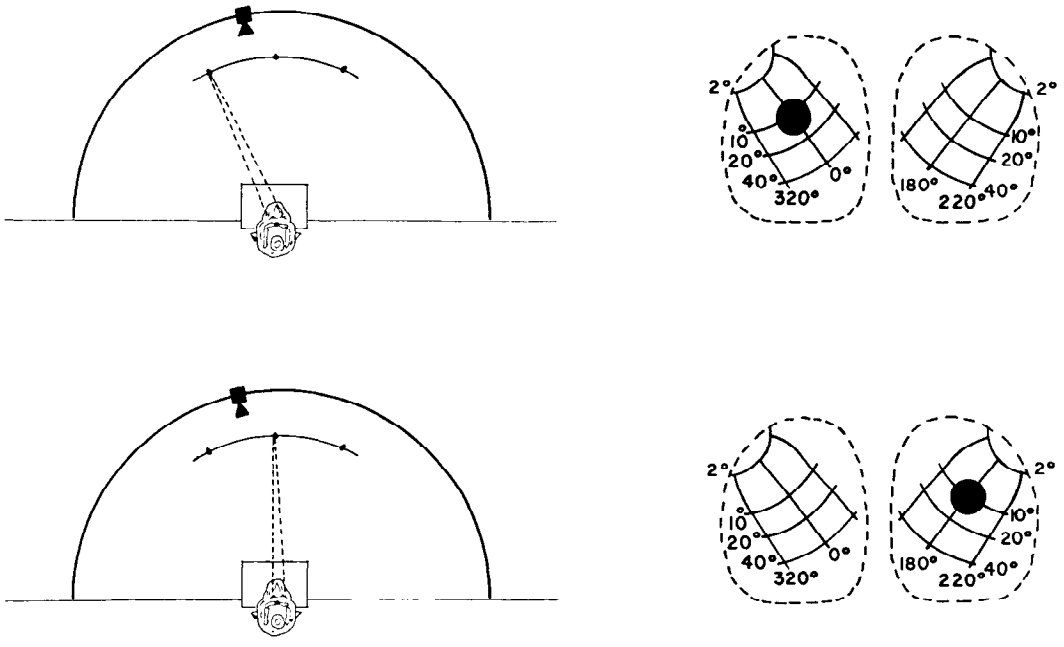

FIG. 14. The shift in the active population of auditory cells in the superior colliculus (SC) with changes in eye position. *Top*: monkey viewing the left fixation light, with the speaker to the right of the fixation position. Auditory cells in the left SC are activated. *Bottom*: when gaze is shifted to the center fixation light (to the right of the speaker), the auditory cells in the right colliculus are now active and code the trajectory of the movement required to look to the target.

the retinotopic map of visual space is the basis for the alignment. However, our data indicate that the sensory maps in the intermediate and deeper layers of the SC are organized in motor coordinates. According to this view, the sensory maps are dynamic, and the receptive fields of collicular neurons shift with relative movements of the eyes, head, and body. The motor map is fixed and mandates a transformation of sensory signals into signals of motor error.

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. ABRAHAMS, V. C. AND ROSE, P. K. Projections of extraocular, neck muscle and retinal afferents to the superior colliculus in the cat: their connections to cells of origin of tectospinal tract. *J. Neurophysiol.* 38: 10–18, 1975.
2. ADDISON, P. D., AITKIN, L. M., MOORE, D. R., AND SEMPLE, M. N. Auditory receptive field organization of neurones in the cat inferior colliculus. *J. Physiol. Lond.* 338: 43, 1983.
3. BALEYDIER, C. AND MAGNIN, M. Afferent and efferent connections of the parabigeminal nucleus revealed by retrograde axonal transport of HRP. *Brain Res.* 161: 187–198, 1978.
4. BIZZI, E. Discharge of frontal eye field neurons during saccadic and following eye movements in unanesthetized monkeys. *Exp. Brain Res.* 6: 69–80, 1968.
5. CHALUPA, L. M. AND RHOADES, R. W. Responses of visual, somatosensory, and auditory neurones in the golden hamster's superior colliculus. *J. Physiol. Lond.* 270: 595–626, 1977.
6. DONALDSON, I. M. L. AND LONG, A. C. Interactions between extraocular proprioceptive and visual signals in the superior colliculus of the cat. *J. Physiol. Lond.* 298: 85–110, 1980.
7. DRÄGER, U. C. AND HUBEL, D. H. Responses to visual stimulation and relationship between visual, auditory, and somatosensory inputs in mouse superior colliculus. *J. Neurophysiol.* 38: 690–713, 1975.
8. DRÄGER, U. C. AND HUBEL, D. H. Physiology of visual cells in mouse superior colliculus and correlation with somatosensory and auditory input. *Nature Lond.* 253: 203–204, 1975.

9. EVINGER, C., BAKER, R., MCCREA, R. A., AND SPENCER, R. Axon collaterals of oculomotor nucleus motoneurons. In: *Progress in Oculomotor Research,* edited by A. Fuchs and W. Becker. New York: Elsevier/North-Holland, 1981, p. 263–270.
10. FRIES, W. Cortical projections to the superior colliculus in the macaque monkey: A retrograde study using horseradish peroxidase. *J. Comp. Neurol.* 230: 55–76, 1984.
11. GOLDBERG, M. E. AND WURTZ, R. H. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* 35: 560–574, 1972.
12. GRAYBIEL, A. M. Direct and indirect preoculomotor pathways from the brainstem: An autoradiographic study of the pontine reticular formation in the cat. *J. Comp. Neurol.* 175: 37–73, 1977.
13. HARRIS, L. R., BLAKEMORE, B., AND DONAGHY, M. Integration of visual and auditory space in the mammalian superior colliculus. *Nature Lond.* 288: 56–59, 1980.
14. HIGHSTEIN, S. M., KARABELAS, A., BAKER, R., AND MCCREA, R. A. Comparison of the morphology of physiologically identified abducens motor and internuclear neurons in the cat: A light microscopic study employing the intracellular injection of horseradish peroxidase. *J. Comp. Neurol.* 208: 369–381, 1982.
15. JAY, M. F. AND SPARKS, D. L. Sensorimotor integration in the primate superior colliculus. I. Motor convergence. *J. Neurophysiol.* 57: 22–34, 1987.
16. 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.
17. JAY, M. R. AND SPARKS, D. L. Auditory and saccade-related activity in the superior colliculus of the monkey. *Soc. Neurosci. Abstr.* 12: 951, 1982.
18. KELLER, E. L. Participation of medial pontine reticular formation in eye movement generation in monkey. *J. Neurophysiol.* 37: 316–320, 1974.
19. KING, A. J. AND PALMER, A. R. Cells responsive to free-field auditory stimuli in guinea-pig superior colliculus: Distribution and response properties. *J. Physiol. Lond.* 342: 361–381, 1983.
20. KNUDSEN, E. I. Auditory and visual maps of space in the optic tectum of the owl. *J. Neurosci.* 2: 1177–1194, 1982.
21. LEICHNETZ, G. R., SPENCER, R. F., HARDY, S. F. P., AND ASTRUC, J. The prefrontal corticotectal projection in the monkey: An anterograde and retrograde study. *Neuroscience* 6: 1023–1041, 1981.
22. MAYS, L. E. AND SPARKS, D. L. Dissociation of visual and saccade-related responses in superior colliculus neurons. *J. Neurophysiol.* 43: 207–231, 1980.
23. MCCREA, R. AND BAKER, R. Evidence for the hypothesis that the prepositus nucleus distributes "efference copy" signals to the brainstem. *Anat. Rec.* 196: 122–123, 1980.
24. MCCREA, R., YOSHIDA, K., BERTHOZ, A., AND BAKER, R. Eye movement related activity and morphology of second order vestibular neurons terminating in the cat abducens nucleus. *Exp. Brain Res.* 40: 468–473, 1980.
25. MIDDLEBROOKS, J. C. AND PETTIGREW, J. D. Functional classes of neurons in primary auditory cortex of the cat distinguished by sensitivity to sound location. *J. Neurosci.* 1: 107–120, 1981.
26. NODA, H. AND SUZUKI, D. A. Processing of eye movement signals in the flocculus in the monkey. *J. Physiol. Lond.* 294: 349–364, 1979.
27. PÖPPEL, E. Comment on "visual system's view of acoustic space." *Nature Lond.* 243: 231, 1973.
28. ROBINSON, D. A. Eye movements evoked by collicular stimulation in the alert monkey. *Vision Res.* 12: 1795–1808, 1972.
29. ROSE, P. K. AND ABRAHAMS, V. C. The effects of passive eye movement on unit discharge in the superior colliculus of the cat. *Brain Res.* 97: 95–106, 1975.
30. SEMPLE, M. N., AITKIN, L. M., CALFORD, M. B., PETTIGREW, J. D., AND PHILLIPS, D. P. Spatial receptive fields in the cat inferior colliculus. *Hear. Res.* 10: 203–215, 1983.
31. 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.
32. 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.
33. STEIN, B. E., MAGALHAES-CASTRO, B., AND KRUGER, L. Superior colliculus: Visuotopic-somatotopic overlap. *Science Wash. DC* 189: 224–226, 1975.
34. 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.
35. WICKELGREN, B. G. Superior colliculus: some receptive field properties of bimodally responsive cells. *Science Wash. DC* 173: 69–72, 1971.
36. WISE, L. Z. AND IRVINE, D. R. F. Auditory response properties of neurons in deep layers of cat superior colliculus. *J. Neurophysiol.* 49: 674–685, 1983.