Exp Brain Res (1995) 103:227–242


ORIGINAL PAPER

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# Effects of eye position on saccadic eye movements and on the neuronal responses to auditory and visual stimuli in cat superior colliculus

Received: 2 August 1994 / Accepted: 21 November 1994

**Abstract** Many neurons in the deeper layers of the superior colliculus (SC) respond to multiple sensory inputs – visual, auditory, and somatic – as well as provide signals essential for saccadic eye movements to targets in different modalities. When the eyes and pinnae are in primary position, the neural map of auditory space is in rough topographic alignment with the map of visual space, and if the auditory map is based solely on head-pinna coordinates, any changes in eye position in the orbit will cause misalignment of the maps. We investigated the effects of eye position on the response of sound-sensitive neurons in the SC of cats because previous work on cats and on monkeys had suggested the possibility of species differences in the representation of auditory signals in the SC. We also investigated the effects of eye position on the accuracy of saccades to auditory, visual, and bimodal stimuli. All studies were conducted in alert, trained cats with the head restrained in a fixed position. Neuronal and behavioral responses were studied during periods when the eyes were steadily directed to different positions relative to the position of the sound. Cats showed partial compensation for eye position in making saccades, regardless of the modality of the target, and they showed similar patterns of error in saccades to auditory and visual targets. These behavioral data are consistent with coding the location of visual and auditory targets in the same coordinate system. In the vast majority of intermediate-layer neurons, eye position significantly affected the number of spikes evoked by sound stimuli. For most of these neurons, changes in eye position produced significant shifts in the speaker location producing maximal response. In some neurons, eye position significantly facilitated the magnitude of neuronal response evoked by sounds from a variety of speaker locations. Because few pinna movements could be detected, it is unlikely that these changes in neuronal response could be due to changes in the position of the pinnae. Our results indicate that the deep layers of the SC contain an eye-centered representation of sound location. Because eye position did not affect the percentage of neurons exhibiting multimodal integration, visual and auditory maps appear to remain integrated in the SC even when the eyes are directed eccentrically. Examination of the effects of eye position on neuronal responses to visual stimuli revealed that a substantial minority of neurons showed quantitative changes in the magnitude of response to visual stimuli when the retinal locus of stimulation was held constant.

**Key words** Vision · Audition · Superior colliculus
Saccade · Multisensory convergence · Cat

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## Introduction

Information about multiple sensory events converges on cells in a number of structures in the brain, including the intermediate and deep layers of the superior colliculus (SC) or optic tectum. Many cells in these layers respond to auditory, somatosensory, vestibular, and proprioceptive inputs as well as to visual stimuli. Moreover, neurons responsive to inputs from the major modalities are organized topographically, and the maps of different modalities are in correspondence when the eyes are centered in the orbit (Stein and Meredith 1993). Although Sparks and colleagues have suggested that these layers are organized in motor error coordinates (e.g., Mays and Sparks 1980; Sparks 1986), it is also possible that various coordinate systems may coexist within these layers. A variety of models for such sensorimotor translations have been proposed.

One strategy for distinguishing between sensory and motor contributions to the topographic maps in the SC is to map receptive fields when the eye is directed to different positions in the orbit and then to observe whether the

sensory maps shift with changes in eye position. If the multiple maps are independent maps of sensory space, changes in eye position should produce shifts of visual, but not auditory, receptive fields. On the other hand, if deep-layer neurons are in oculomotor coordinates, the location of auditory receptive fields would shift with changes in eye position. In the monkey SC, Jay and Sparks (1987) have found that the responses of most sound-sensitive SC neurons are affected by eye position. Some of these cells are dramatically affected: their discharge is better predicted by the position of the eyes relative to the target than by the position of the target relative to the head. These results provide strong support for the idea that the deep layers of the SC contain an eye-centered map of motor error (Sparks 1986). In contrast, two studies in cats indicate that changes in eye position do not produce shifts in the position of auditory receptive fields: auditory receptive fields of anesthetized and paralyzed cats have been reported to be unaffected by passive displacements of the eyes (Nelson et al. 1986), and, in alert cats, auditory receptive fields of a small sample of neurons were not found to shift with voluntary changes in eye position (Harris et al. 1980). It is possible that the results obtained by Harris et al. in the cat are attributable to species differences in the coding of sound location in the SC, and thus the generality of the conclusions of Jay and Sparks in monkey needs to be established. The major goal of this study was to evaluate the effects of eye position on the responses of sound-sensitive cells in the SC of alert cats. In order to obtain consistent oculomotor performance throughout the course of these experiments, the cats were first trained in several behavioral tasks (Peck 1989, 1990).

The second purpose of these experiments was to determine whether voluntary shifts in eye position would affect the accuracy of saccades to sounds. If the accuracy of saccadic eye movements toward auditory targets depends on eye-position-independent maps of sound location within the SC, as implied by the lack of influence of eye position on neuronal responses to auditory stimuli in the study of Harris et al. (1980), then cats should make systematic errors whenever the eyes are deviated in the orbit. Finally, the results obtained with auditory stimuli led us to reexamine the effects of eye position on the responses of the SC neurons to visual and bimodal stimuli.

Preliminary reports of some of these observations have appeared elsewhere (Peck and Wartman 1989; Peck et al. 1993).

## Materials and methods

These studies were conducted on six adult cats. All of the procedures used were approved by the University of Missouri-St. Louis Animal Care and Use Committee and complied with United States Public Health Service guidelines for animal care and use. All surgical procedures necessary to prepare the cats for eye movement recording and neurophysiological experiments were performed under deep pentobarbital sodium anesthesia. A scleral search coil was implanted under the conjunctiva of one eye and a head holder was secured to the skull with stainless steel skull screws in order to permit painless restraint of the head. After recovery from surgery, each cat was gently and gradually accustomed to head restraint before proceeding with the training procedures described below. All cats accepted head restraint without struggling or discomfort, as evidenced by their ability to carry out the behavioral tasks. Each cat was monitored continuously on a closed-circuit infrared video system in order to ensure that it was working comfortably throughout each session and to verify that extraneous movements were not occurring. Experimental sessions typically lasted 2–3 h and were discontinued if the cat became restless or sleepy.

### Stimulus display

All visual and auditory stimuli were presented along the circumference of a horizontally oriented hoop, 0.8 m in diameter, centered on the cat's median sagittal plane at the level of the interaural axis. The recording chamber (2.5×4.7×2.2 m) was darkened. Visual stimuli (amber light-emitting diodes, LEDs, luminance 0.34 cd/m$^2$) were mounted at 10° intervals from straight ahead of the cat out to 60° on each side. Small loudspeakers were mounted just below each LED. A variety of tones, clicks, and environmental noises were used when searching for cells. For quantitative testing, auditory stimuli were bursts of broadband noise (200–20000 Hz, 52 dB sound pressure level, SPL, on a background of 35 dB, measured with a hand-held sound-level meter at the position of the cat's head). The walls of the recording chamber were lined with egg-crate acoustic foam panels. Background illumination, when used, was less than 0.005 cd/m$^2$. For bimodal stimulation, auditory and visual stimuli were presented simultaneously at the same location.

### Behavioral methods

Preliminary calibrations of the search coil were obtained during the process of adapting each cat to the recording situation. The cat was placed so that the central target (0°) was straight ahead of the cat and aligned with its median sagittal plane. As the cat became accustomed to head restraint, food rewards were given whenever eye movements were made in the general direction of a visual target by setting an electronic window around each target position. Search-coil calibration values were adjusted according to the performance of each cat. As performance improved, the size of the window was decreased and the length of the required fixation period was increased until the cats were consistently making accurate fixation eye movements to visual targets at a minimum of three different locations (generally 0° and 10° to the left of primary position, and 10° to the right of primary position). Target duration varied from 500 ms to 3 s. After cats became proficient in the *fixation task*, they were trained on a *saccadic tracking task*, in which the fixation target was extinguished and a second target (the saccade target) appeared 125–650 ms later. Duration of the saccade target varied from 250 ms to 1.5 s. Reward in this task was contingent on fixating the first target, making a saccade to within a few degrees of the second target within a specified period of time (usually 500 ms), and maintaining fixation on the second target for a specified period (500 ms to 2 s). Visual, auditory, and bimodal stimuli were used as fixation targets and saccade targets in different blocks of trials. To discourage anticipatory saccades, in about one trial in every five, the second target reappeared at the location of the fixation target. Two cats were also trained in a *delayed saccade task*, in which reward was contingent on making a saccade to the auditory target after a delay of 200–500 ms. However, because mean saccade latencies ranged between 190 and 200 ms even with optimal "gaps" between the offset of the fixation target and the onset of the saccade target, we combined data collected during both types of saccade tasks.

For both behavioral and physiological experiments, we used target locations that were within the oculomotor range of the cat from primary position (±20°). In order to induce the cats to make

eye movements regularly to auditory targets, we used large eye-position windows (±10°), similar but slightly smaller than those used for studies of saccadic eye movements to auditory targets in primates (Jay and Sparks 1989). Thus, the cats were not rewarded for random eye movements, but only for those in the general direction of the target. Use of a large window ensured that the cats were not forced to compensate for the position of the eye in order to obtain a reward. Data from both correct and incorrect trials were saved for analysis.

## Physiological methods

Insulated tungsten microelectrodes were positioned stereotaxically and advanced slowly with a remotely controlled microdrive to isolate single cellular waveforms. Neuronal activity was amplified and filtered conventionally. We monitored the raw activity signal and the output of a window discriminator (Bak, model DS-1) simultaneously on an oscilloscope and on an audio monitor. Visual and auditory targets were used as search stimuli while advancing the microdrive and attempting to isolate cells. We attempted to use visual, auditory, and bimodal stimuli to test each isolated neuron, although some cells were lost before the entire set of combinations could be completed. Trials of various types were interleaved to control for long-term changes in excitability. It was difficult to collect many trials in complete darkness without compromising task performance. Therefore, to avoid influence of inadvertent visual stimulation on neuronal responses, most neurons were studied briefly in complete darkness, as well as with dim background illumination. In one cat, all neurons were studied in complete darkness.

Cats were continuously monitored by an infrared video system to detect any movements other than those of the eyes. In two cats, the positions of the external ears were recorded on videotape and a search coil was mounted on one ear to record pinna movements. Although we could easily elicit pinna movements with uncontrolled stimuli, they habituated readily and almost never occurred with controlled auditory stimuli. During our experiments, changes in the position of the external ears were so slight that we were unable to measure them.

Isolated units were passed through a time-amplitude window discriminator, and the time of occurrence of the pulses produced by the discriminated unit was recorded to a precision of 0.1 ms by a general-purpose laboratory computer (DEC PDP 11/73 or Macintosh II). The computer controlling the behavioral task produced a trigger pulse 500 ms before each trial in order to initiate data acquisition. The horizontal and vertical coordinates of eye position and the positions of the visual and auditory targets were digitized at 200 Hz. Spike discharge patterns of each trial were displayed during the experiment, together with the eye position and stimulus records. The complete file of each trial was then stored.

## Data analysis

Saccades were automatically detected by computer, using a velocity criterion (generally 20°/s), and the results of the selection were checked by human observers. Using the individual calibrations of each animal, coil voltages were converted into degrees of visual angle. Saccade accuracy was quantified by measuring the size and direction of fixation error, which was defined as the difference between the position of the target and the position of the eye after the first saccade. Negative errors mean that the target was to the left of the eye after the first saccade. Mean unsigned (or absolute) errors indicate the precision of the initial eye movement.

Trial-by-trial records of spike counts, instantaneous frequencies, latencies, and other measures of cell activity were obtained using a time window which was set to be appropriate for each cell. For most cells, a 200-ms time window was used to measure changes in activity produced by stimulus onset and offset; shorter time windows were used for cells with very brief responses to sensory stimuli.

### *Cell classification*

Although all data reported in this paper were obtained with the eyes steady in the orbit, cells were also classified according to whether their discharge was related to saccades. Cells lacking sensory receptive fields but having clear movement-related activity were classified as pure movement cells. For some movement cells we had sufficient information on their discharge in relation to memory-guided saccades, and in these cases their discharge was always equivalent before memory-guided saccades and stimulus-guided saccades. Cells lacking movement fields but having stimulus-related activity in the absence of saccades were classified as visual, auditory, or both if their activity was clearly time-locked to presentation of stimuli in that modality during periods when the eyes were steady for at least 200 ms before and after stimulus onset. Visual-movement cells discharged both in response to a visual stimulus in the absence of saccades and before saccades to visual or bimodal stimuli, but did not discharge before saccades to auditory stimuli. Auditory-movement cells discharged both in response to an auditory stimulus in the absence of saccades and before saccades to auditory and bimodal stimuli, but not before saccades to visual stimuli. Visual-auditory-movement cells discharged before saccades to visual, auditory, or bimodal targets and also to unimodal stimuli in the absence of saccades. We did not test responses to learned saccades, nor did we use double-saccade tasks which would allow us to classify cells as quasi-visual (Mays and Sparks 1980).

### *Latency measurements*

Neuronal response latencies were calculated by determining the time from stimulus onset to the first bin in the poststimulus-time histogram in which the mean number of spikes differed by 2 standard deviations from the mean number of spikes per bin in the baseline period (the 500-ms interval before each trial). The midpoint of this bin was taken as the neuronal latency.

### *Statistical analyses*

For all statistical tests, the criterion for statistical significance was $P=0.05$. Because the distribution of response latencies was skewed, nonparametric statistics were used to describe the distribution of latencies and to evaluate the differences in the latency of neuronal responses to visual, auditory, and bimodal targets.

Effects of eye position on neuronal responses to visual and auditory stimuli were first determined from trial-by-trial analyses of each neuron. We then measured the magnitude of the effects of eye position on a sample of neurons and computed population statistics. Because of the loss of our DEC system, it was not possible to complete this analysis for all cells studied. Two-tailed tests were used for all trial-by-trial analyses. One-tailed tests were carried out for population analyses where the experimental prediction was that effects would be greater than zero. To analyze the effects of eye position on the responses of each neuron to auditory stimuli, we performed an analysis of covariance on the number of spikes evoked by sounds at each spatial location as a function of initial horizontal eye position. The null hypothesis was that eye position had no effect on the response to sound. Significant main effects of eye position, without a significant interaction between target position and eye position, indicated an overall *facilitation* of response level as a function of eye position. A significant interaction between target position and eye position indicated a *shift* in the optimal location of an auditory stimulus with respect to the eye.

To measure the extent of the shift in receptive field location as a function of eye position, we determined the speaker location at which each neuron responded most vigorously for each set of eye positions. We then calculated a percentage shift (%S), which was defined as $\%S=100\cdot(OSE-OSC)/(EEP-ECP)$, where OSE is the optimal speaker location for a set of trials in which steady eccentric eye position (EEP) was maintained and OSC is the optimal speaker location for a set of trials in which steady central eye posi-

tion (ECP) was maintained. An index of zero indicates that the auditory receptive field of the cell shifted less than the separation of the speakers. An index of more than zero implies that the receptive field shifted in the direction of the change in eye position, and an index of less than zero implies that the receptive field shifted in the opposite direction.

We also calculated the percentage facilitation (%F) of responses by changes in eye position, defined as

%F=100·(MRE-MRC)/MRC,

where MRE is the mean number of spikes in response to sound at the optimal location for the set of trials in which steady eccentric eye position was maintained and MRC is the mean number of spikes in response to sound at the optimal speaker location for the trials in which steady central eye position was maintained. An index of zero indicates that changes in eye position had no effect on the magnitude of the response to sound. An index of more than zero shows that the cell responded more vigorously when the eyes were directed eccentrically, and an index of less than zero shows that the cell responded more vigorously when the eyes were centered in the orbit.

Analysis of covariance was also used to evaluate the effect of eye position on bimodal interactions. Responses to bimodal stimuli were compared with the responses to stimuli in the more effective single modality. Significant main effects of modality indicated that the number of spikes evoked by bimodal stimuli was significantly different from the number evoked by the more effective unimodal stimulus, regardless of the position of the eye. Significant effects of eye position indicated that the overall number of spikes evoked by both unimodal and bimodal targets was greater at some eye positions, and significant interactions between modality and eye position indicated that the strength of bimodal interactions varied with eye position.

Effects of eye position on visual responses of individual neurons were assessed by multiple analysis of covariance, with the retinal coordinates (horizontal and vertical) of stimulus position and of eye position as the covariates. Significant main effects of horizontal or vertical eye position, in the absence of significant interaction between retinal stimulus position and eye position, indicated that the overall number of spikes was greater at some eye positions, independent of the retinal position of the visual stimulus. Significant interactions between retinal stimulus position and eye position indicated that there was either a shift in the optimal retinal location of visual stimuli or gating of visual input by eye position.

### Histology

After completion of the daily recording sessions, the cats were killed with an overdose of pentobarbital sodium and perfused with saline, followed by buffered formalin. Frozen coronal sections were taken and stained with thionin for reconstruction of recording sites marked with electrolytic lesions. The long duration and large number of electrode penetrations restricted individual identification of most recording sites. Stereotaxic and microdrive coordinates of identified penetrations allowed the reconstruction of the locations of the majority of unmarked sites in three of the cats. In the other three cats, a grid system was used to guide electrode tracks. The boundaries of the grid were verified to be within the SC, and the depth of each neuron was recorded, but the absolute medial-lateral and anterior-posterior coordinates of each cell were not obtained. These cells were assigned to superficial or deep layers on the basis of their physiological responses, together with the responses of other cells in the same penetrations.

## Results

### Saccades in response to auditory targets

In order to determine whether the cats were able to make accurate saccades to auditory targets, we analyzed all available data from both correct and incorrect trials in five cats. Because the location of the targets differed in azimuth, but not in elevation, we will emphasize the patterns of *horizontal* fixation errors. FigureÊ1 illustrates the horizontal component of saccades in response to sound stimuli on eight trials in one cat (cat P). In the four trials illustrated in the upper panel of Fig.Ê1, the sound was located 20° to the right of the cat's midline; in the lower panel, the sound was presented 10° to the cat's right. Despite considerable variation in the initial position of the eye and in the latency of the targeting saccade, these data indicate that cats can make reasonably accurate saccades to sounds from a wide range of initial eye positions. Saccades in the wrong direction were rare and, when they occurred, were made toward the primary position of the eye in the orbit (cf. Kurylo et al. 1992).

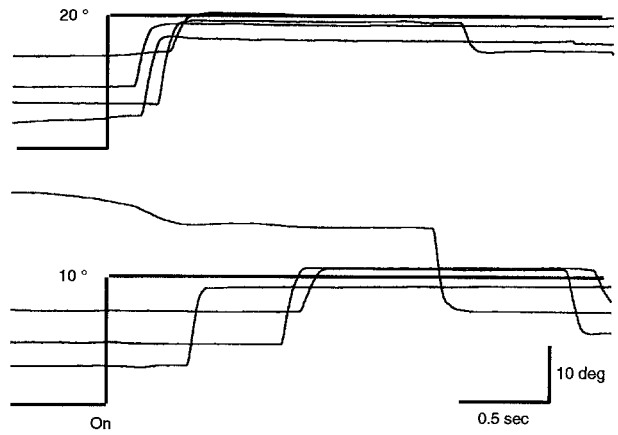


**Fig. 1** Horizontal components of targeting saccades from eight typical trials in cat P. Traces are synchronized on sound onset, shown by the *vertical line*. Upward deviations indicate rightward eye movements. Time of sound onset is shown by the upward deflection of the stimulus trace (*thicker line*), and location of the sound source is shown by the horizontal position of the stimulus trace. All saccades ended near the target, despite the fact that they were initiated from positions varying by nearly 30°

To measure the effects of initial eye position on saccadic accuracy, we plotted the magnitude of horizontal fixation errors as a function of initial horizontal eye position. If sounds are localized in head-centered coordinates by the oculomotor system, then for each target position fixation error should be equal but opposite to initial eye position using our measurement conventions. Only when the eyes are centered in the orbit would saccadic error signals be correct. For example, if a target is located at +10° (10° to the right of primary position) and the cat's eyes are at 0°, a head-centered coordinate system would indicate an initial error of +10° and the cat would move its eyes 10° to the right. However, with the same target, if the cat's eyes were at –10° (10° to the left of primary position), the cat would move its eyes to 0°, making a fixation error of +10°. Figure 2 illustrates the effect of initial eye position on horizontal fixation errors of four cats when auditory stimuli were presented at +10° (filled symbols) and at –10° (open symbols). Data from both incorrect and correct trials are included. The slopes of the

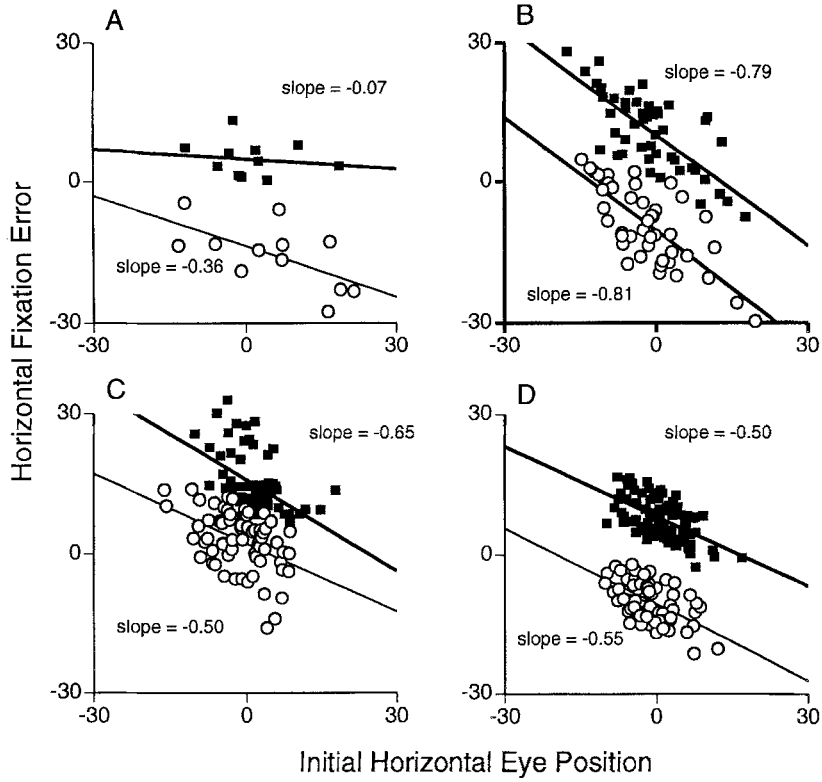


**Fig. 2A-D** Errors in fixation eye position after saccades in response to sounds. Each point represents data from a single trial. Initial horizontal eye position is the horizontal coordinate of eye position at the time of target onset. *Negative numbers* indicate leftward eye positions; *positive numbers* indicate rightward eye positions. Horizontal fixation error is the difference between target position and eye position after the first saccade occurring after target onset. *Negative numbers* indicate that the target was to the left of the eye; *positive numbers* indicate that the target was to the right of the eye. *Filled symbols* indicate trials when the sound was presented 10° to the cat's right (+10°); *open symbols* indicate trials when the sound was presented 10° to the left (-10°). *Solid lines* represent the best-fit linear regression equation for each data set. Trials with different locations of the sound source were randomly intermixed. **A** Cat P; **B** cat I; **C** cat O; **D** cat Sk. Note that cat P showed the most compensation for initial horizontal eye position at these two speaker locations

best-fit linear regression equations for these data ranged from –0.07 (cat P, auditory target at +10°) to –0.81 (cat I; auditory target at –10°), with a mean of –0.44. When the same analysis was repeated with visual targets, the mean slope of these functions was –0.46; with bimodal targets, the mean slope was –0.31. Across cats and target locations, the slopes of the regression functions differed consistently both from –1.0 (the value which would be obtained if there were no compensation for initial eye position) and from zero (the value which would be obtained if there were complete compensation). Addition of nonlinear components did not improve the degree of fit significantly.

The data presented in Fig. 2 show that these cats sometimes made very large errors in a saccadic task. In order to determine whether this could indicate that they were performing the task randomly, we plotted the frequency and extent of horizontal fixation errors, as illustrated in Fig. 3 for auditory targets at +10°. Thinner lines represent data from trials in which the eyes were initially directed less eccentrically than +10°, while heavier bars represent data from trials when the eyes were directed *more* eccentrically than the target. Although there was individual variability across the cats in the extent of localization errors, in no case were the errors randomly distributed across the range of the eye position error window (±10°) used for reward. Instead, each of the cats showed a tendency to undershoot targets when the eyes were less eccentric than the target, as distinguished by a greater concentration of positive (rightward) errors when targets were located to the right (Fig. 3) and a greater concentration of negative (leftward) errors when the targets were located to the left (not illustrated).

If the saccadic oculomotor system codes sound location in head-pinna-centered coordinates, incorrectly directed saccades to auditory targets should be the rule if saccades are initiated from eye positions more eccentric than the location of the sound. This would result in leftward errors for sounds presented to the right: for example, if the eyes are directed 15° to the right (+15°) and the sound stimulus is presented at +10°, the cat should make a saccade to a position 25° to the right (+25°), thus producing a fixation error of –15°. Although we examined those data carefully, we did not find that directional errors were typical in any of the cats. All of the saccades plotted with heavy lines in Fig. 3 were correctly directed. One cat (cat O) showed a tendency to overshoot auditory saccade targets (ending closer to primary position) when saccades to targets at +10° were initiated from an eye position more eccentric than the target, and one cat (cat I)

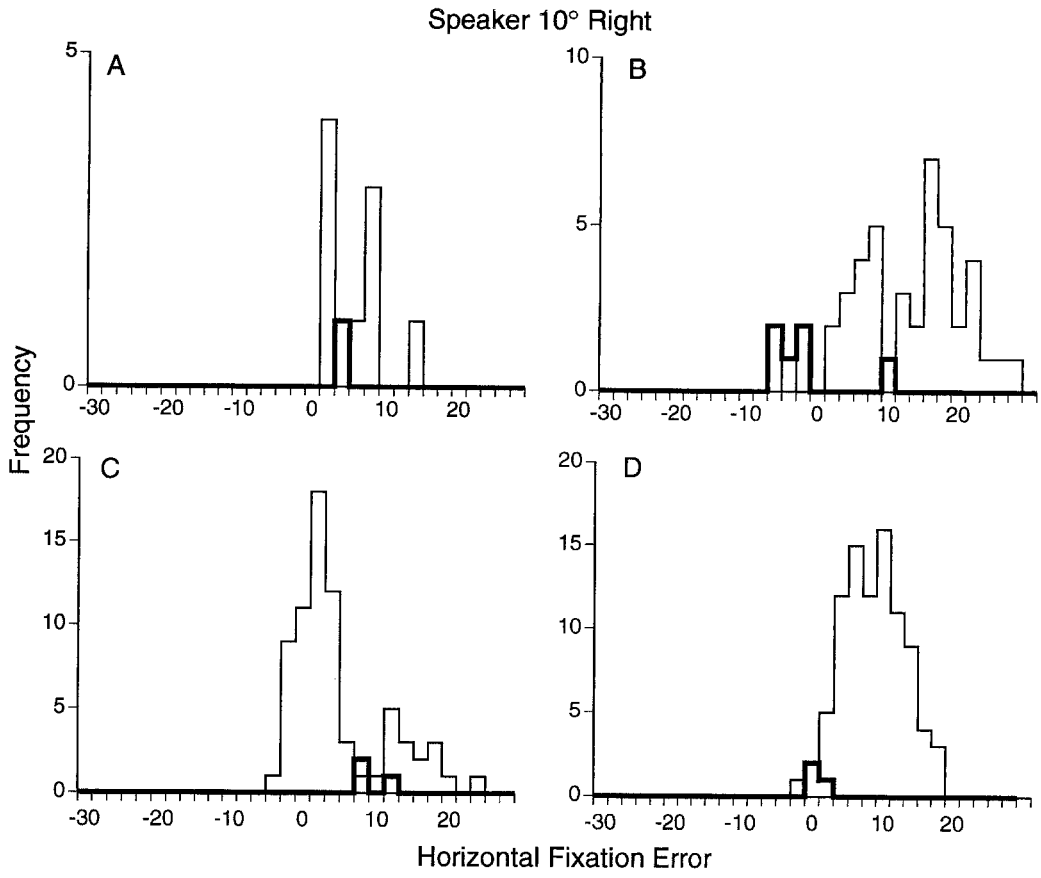


**Fig. 3A-D** Frequency of horizontal fixation errors for trials when the sound stimulus was presented 10° to the cat's right (+10°). Trials in which initial horizontal eye position (at the time of target onset) was less eccentric than the target are indicated by *thin lines*; trials when the initial horizontal position of the eye was more eccentric than the target are indicated by *thick lines*. (Same cats as in Fig. 2)

tended to end such saccades eccentric to the target (i.e., to undershoot), while the other two cats ended such saccades near the target.

To compare saccadic errors across conditions without having rightward and leftward errors cancel each other, we computed the mean of the absolute value of saccadic errors. The means of these absolute values were comparable for saccades made to visual, auditory, and bimodal stimuli. Regardless of target modality, errors were lowest for targets within 10° of the cat's midline and increased significantly when targets were presented at 20° eccentricity (for saccades to auditory targets, $F$=266.34, $P$=0.0001). When averaged across target locations, two cats had larger errors for saccades to sounds than for saccades to visual targets, while two had larger errors for saccades to visual targets than for saccades to sounds. Moreover, while three of the four cats showed greater variability in the accuracy of their saccades to sounds, as measured by the standard error of their mean absolute fixation errors, only one of the four had a greater coefficient of variation for saccades to sounds than for saccades to lights. Thus, there were relatively few differences in saccadic errors across target modality.

## Neuronal responses to auditory, visual, and bimodal stimuli

Activity patterns of 140 neurons could be related to the presentation of auditory stimuli when the eyes were steady in the orbit. Sensory stimuli were presented at random locations within the oculomotor range. Because the stimuli occurred unpredictably, at different times and locations, the cats were encouraged to scan the environment and thus to assume eccentric eye positions. Head position was fixed and aligned with the center (0°) speaker. Speaker locations were measured with respect to the head. Cells were classified as responding to a given stimulus modality if their discharge was time-locked to the onset or offset of stimuli in that modality when the cat's eyes were steady (see Materials and methods).

**Table 1** Neuronal response latency

| | Median | Interquartile range |
|---|---|---|
| Speaker | 50 | 30–90 |
| LED | 70 | 40–100 |
| Speaker and LED | 65 | 40–120 |

**Table 2** Number of visually responsive cells showing effects of eye position ($P \leq 0.05$)

| | Interaction between eye position and receptive field position | |
|---|---|---|
| | Significant | Nonsignificant |
| Main effect of eye position | | |
| Significant | 9 | 5 |
| Nonsignificant | 5 | 36 |

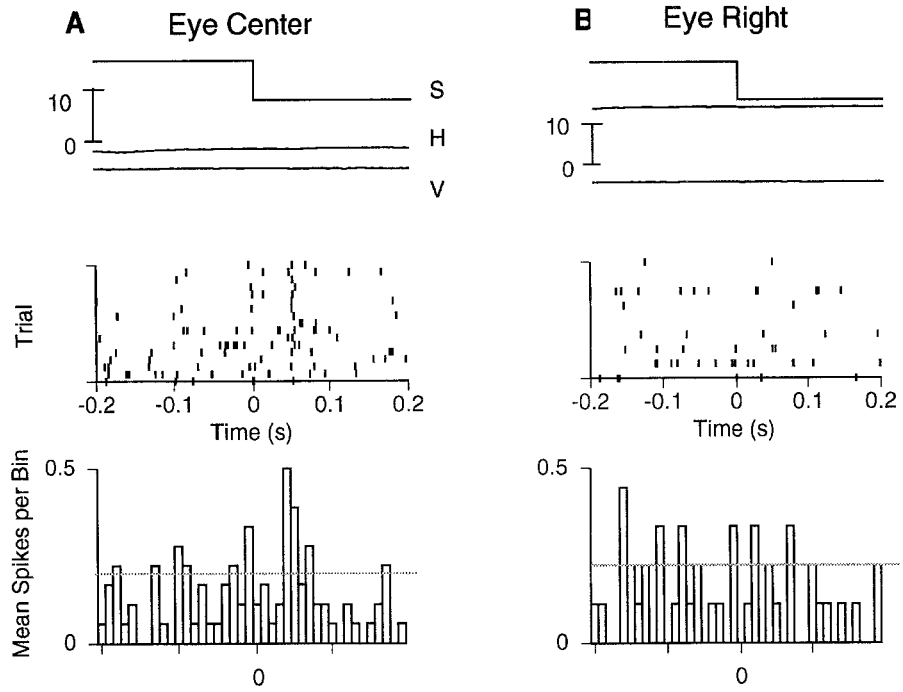


**Fig. 4A,B** Effects of eye position on the responses of a deep-layer neuron to sound offset. **A** Responses to sound offset when eye position was steady and centered (0±5°) in the orbit. All events are aligned on the time of sound offset, shown as time zero on the *bottom scale*. The sound was on throughout the first 200 ms, as indicated by the initial positive deflection of *trace S*. *H* and *V* indicate the horizontal and vertical position of the eye throughout this portion of a typical trial. Neuronal activity (*raster displays*): Each *small vertical line* represents the time of occurrence of an action potential, and each *row* (or raster) represents the response of this cell on one trial. The histograms sum the responses in the rasters directly above. The *vertical scale* of the histogram indicates the mean number of spikes in each 10-ms bin for both **A** and **B**. The *horizontal dotted line* across the histogram indicates the mean number of spikes plus 1 SE of the mean number of spikes per bin in the baseline time period. **B** Eye and stimulus traces, rasters, and histogram for trials when the horizontal position of the eye was steadily directed to the right (10±5°) for 200 ms before and after the time of sound offset

Table 1 shows the median response latencies and interquartile ranges for neuronal responses to visual, auditory, and bimodal stimuli. We did not attempt to equate the intensity of visual and auditory targets, nor did we equate the effectiveness of these stimuli. The median latency of responses to auditory stimuli (uncorrected for sound propagation time) was 50 ms, while the median latency of responses to visual stimuli was 70 ms and the median latency to bimodal stimuli was 65 ms. Response latencies to visual stimuli were significantly longer than those to auditory stimuli (Mann-Whitney $U$=115.5, $P$<0.001). Although our auditory latencies are longer than typical values for sound-responsive neurons in the SC of anesthetized cats (e.g., Hirsch et al. 1985; Meredith et al. 1987), they are comparable with those reported for auditory neurons in the SC of the alert macaque (Jay and Sparks 1987).

*Effects of eye position on responsiveness to auditory stimuli*

Significant effects of eye position on neuronal responses evoked by sounds were found in 107 (76%) of 140 neurons. Eye position affected sound-evoked responses of neurons in each of the major sound-responsive classes: those responding in relationship to eye movements (auditory-visual-movement) and those without such responses (auditory and auditory-visual). Neither of the auditory-movement neurons tested showed a significant effect of eye position on its sound-evoked discharge.

Figures 4 and 5 illustrate the sound-evoked discharge patterns of two representative deep- layer neurons recorded from the SC. The response of an SC neuron to the offset of an auditory stimulus is illustrated in Fig. 4. Although this neuron responded consistently to presentation of auditory stimuli in the frontal hemifield when the eyes were centered in the orbit (Fig. 4A), it gave weaker and less consistent responses to identical stimuli when the eyes were directed to the right (Fig. 4B). When the eyes were centered in the orbit, this neuron responded best to sounds presented 20° to the left; when the eyes were directed 10° to the right, sounds at 10° left evoked the most vigorous responses.

The cell illustrated in Fig. 5 responded to sound onset at an optimal location with latencies between 20 and 40 ms, as illustrated in Fig. 5A and C. Its auditory receptive field did not include 0° when the eyes were centered in the orbit, as illustrated in Fig. 5D, but it responded well to sounds at 0° when the eyes were 8° to the right, as illustrated in Fig. 5C. Similarly, while this neuron responded well to sounds at 10° to the left when the eyes were centered in the orbit, as illustrated in Fig. 5A, it did not respond to sounds at the same location when the eyes were directed 7° to the right (Fig. 5B). For this neuron, the magnitude of sound-evoked responses was greatest

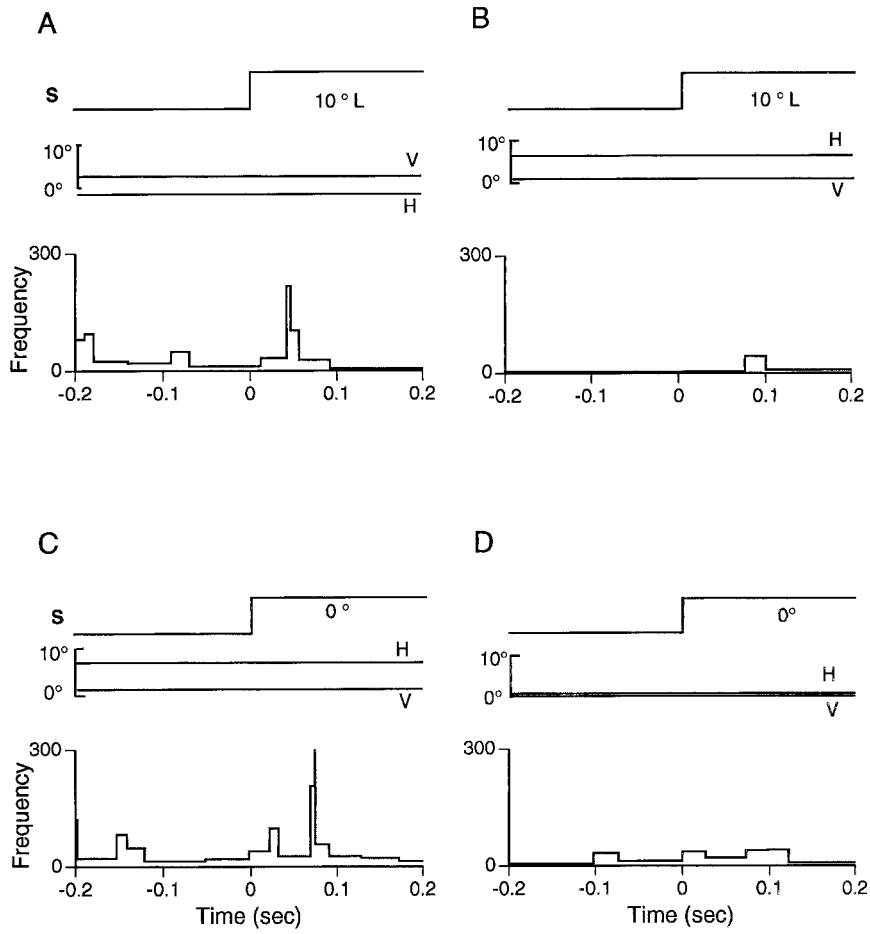


**Fig. 5A-D** Activity of a superior colliculus (SC) neuron which responded to sound onset. All events are aligned on the onset of the sound (*S*) stimulus, indicated by an upward deflection of the *top trace*. *H* and *V* indicate horizontal and vertical eye position, respectively, and the histogram illustrates the instantaneous firing rate of the cell; on the abscissa, zero is the time of sound onset. This cell responded well to sounds when the eyes were 9–10° to the right of the sound (**A, C**) but not to sounds at the same locations when the eyes were directed further from the location of the sound (**B**) or closer to the direction of the sound (**D**). The eyes were within 1.5° of primary position in **A** and **D**; in **B** and **C**, they were 7–8° to the right

when the speaker location was 8–10° to the left of the position of the eye in the orbit.

To quantify these data, we plotted the mean number of spikes in the first 200 ms. following stimulus onset or offset as a function of speaker position and also as a function of motor error (the difference between speaker position and eye position at the time of target presentation). Most neurons showed the pattern of response illustrated in Fig. 6A,B: changes in eye position were paralleled by compensatory shifts in the location of effective auditory stimuli, and discharge rates for different speaker positions differed systematically at different eye positions (Fig. 6A). When the magnitude of the shift in receptive field location was approximately equal to the magnitude of the shift in eye position, discharge rates overlapped well when plotted as a function of motor error (Fig. 6B).

A smaller number of neurons showed the pattern of response illustrated in Fig. 6C,D: their sound-evoked discharge was more vigorous when the eyes were within a certain range of positions in the orbit. As the position of the eye in the orbit changed from trial to trial, the responsiveness of these cells to sounds presented from a range of speaker locations changed dramatically; thus, in these cells, changes in eye position produced an overall *facilitation* in the magnitude of response to auditory stimuli. Ten neurons showed significant facilitation in response level without a significant shift in the most effective speaker location.

The mean value for %S was 62.1 and that for %F was 25.3 for a sample of 51 neurons. Because we had predicted that auditory receptive fields would shift in the direction of the eyes, it is appropriate to use a one-tailed statistical test for %S; however, we used a two-tailed test for %F because we could not make an a priori prediction of its direction. Both %S and %F differed significantly from zero (for %S, $t$=1.84, $P$=0.04; for %F, $t$=2.54, $P$<0.01).

In order to determine whether the patterns of modulation and shifts in optimal speaker location could be due to changing levels of excitability of the cells, we normalized length of the baseline period to equal length of the poststimulus response window, computed the number of spikes in that interval, and subtracted them from the number of spikes in the poststimulus response window of the same trial. There were only slight differences in the effects measured with and without subtraction of background activity.

### *Distribution of eye-position-error signals*

The optimal location of sound stimuli with respect to the eye showed systematic changes as a function of the re-

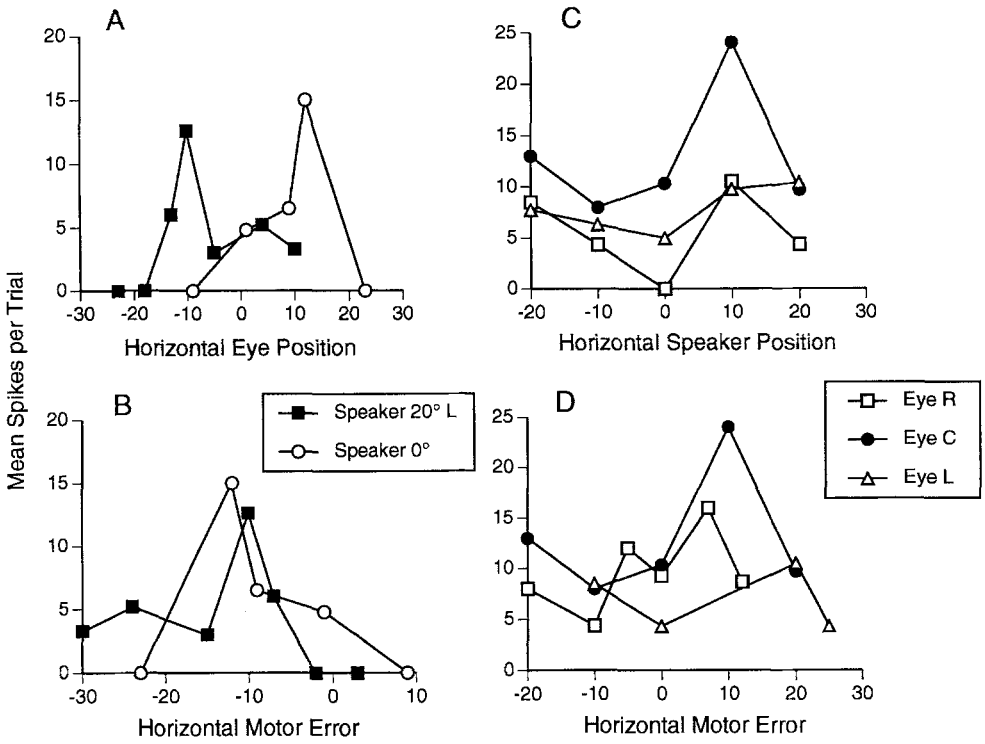


**Fig. 6A-D** Effects of eye position on the responses of two SC neurons to sounds. **A** Mean number of spikes in the first 200 ms. after sound onset when sounds were presented 20° to the catÕs left (*filled squares*) or from straight ahead (0°, *open circles*). Voluntary changes in the horizontal direction of gaze had similar effects on the responses of this cell to sounds from either speaker: the response was most vigorous when the eyes were about 10° to the right of the speaker and declined when the eyes were directed either further from the speaker or closer to it. **B** Data in **A** are replotted as a function of motor error (the distance between the eye and the target); responses to the two speaker locations are better aligned when plotted in motor error coordinates. **C, D** Data from a neuron showing overall facilitation of response as a function of eye position. **C** plots the mean number of spikes in the first 200 ms after the onset of a sound source from one of five different locations (20° to the cat's left, 10° left, 0°, 10° right, and 20° right) when the eyes were within ±5° of primary position (*filled circles*), eccentric to the left (−10±5°; *open inverted triangles*), or eccentric to the right (10±5°; *open squares*). For each speaker position, the number of spikes evoked by sound is greatest when the eyes are centered in the orbit. **D** Data in **C** are replotted as a function of motor error

cording site in the SC. At anterior recording sites, neurons responded optimally to sounds presented in close alignment with current eye position (Fig. 7B,C), with occasional neurons responding best to sounds which were presented ipsilateral to the current position of the eye in the orbit (Fig. 7A). More posteriorly located neurons responded best to sounds presented contralateral to current eye position (Fig. 7D,E). The map in the upper right of Fig. 7 indicates the location of the recording sites in a horizontal map of the SC; the drawing of the horizontal and vertical meridians is based on the work of McIlwain (1983). Because speaker locations were separated by 10° increments, it was not possible to determine whether sounds at intermediate locations would have been more or less effective, and because we only presented targets within the cat's oculomotor range, we do not know whether the cells would have responded to sounds at more eccentric locations. Thus, we cannot determine whether our auditory data are precisely aligned with the visual map when the eyes and pinnae are in primary position.

We plotted the distribution of a sample of 32 sound-responsive neurons according to the depth of the recording site. Only 10 of the neurons whose recording sites could be located showed significant effects of eye position; 7 of these neurons were recorded in the middle third of the intermediate gray layer, 2 were found in the top third, and only one was located in the lower third. Chi-square tests for location revealed that this distribution differed significantly from that of intermediate gray neurons for which eye position did *not* have a significant effect on response to auditory stimuli (overall $X^2=5.83$, two-tailed $P=0.05$; comparing the frequency of cells in the upper third and middle third, $X^2=12.62$, two-tailed $P<0.01$; comparing the frequency of cells in the lower third and middle third, $X^2=41.3$, two-tailed $P<0.01$). Units which were not affected by eye position were distributed more uniformly in the intermediate gray layer; a few were recorded in the deep gray layer.

## Neuronal responses to bimodal targets

Cells were classified as showing bimodal interactions if their responses to simultaneous visual and auditory stimuli were significantly different from their responses to

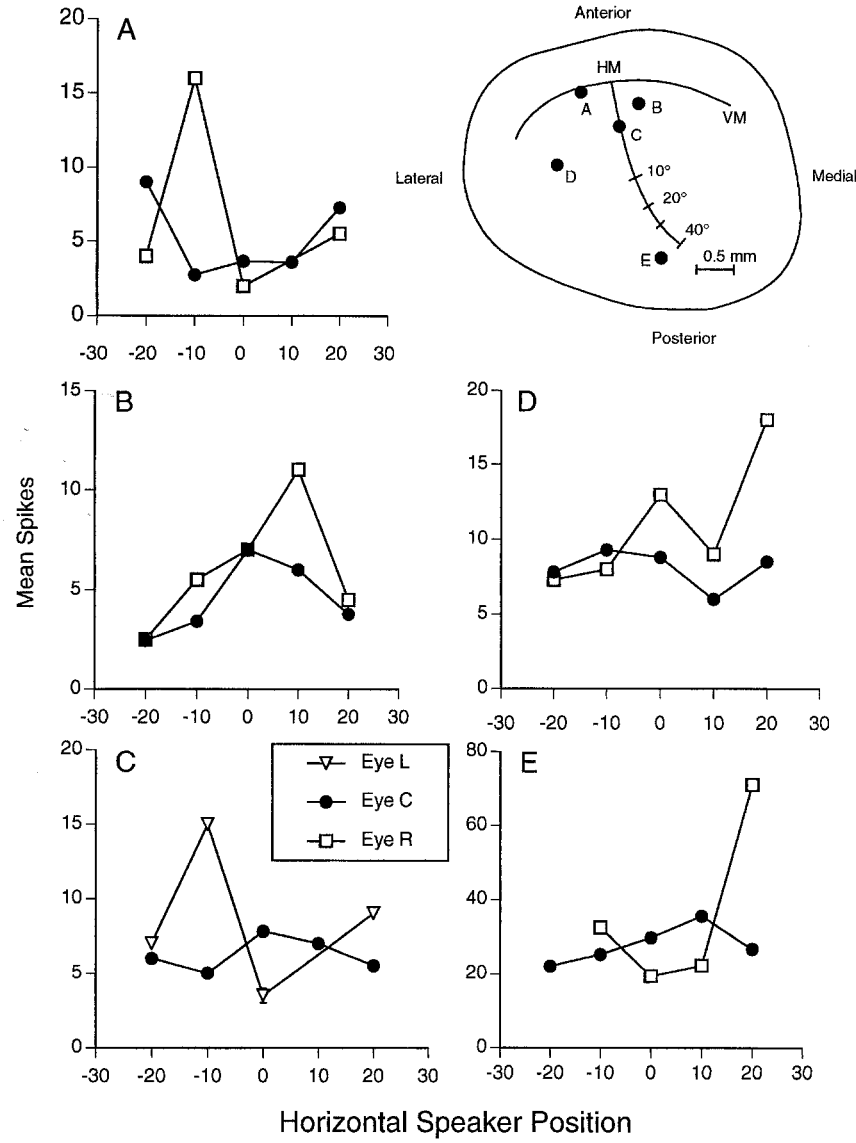


**Fig. 7A-E** Shifts of the optimal location of sound stimuli with changes in eye position for five neurons recorded at different locations in the SC. Responses were obtained during periods when the eye was steady in the orbit for at least 200 ms before and after sound onset. *Inset at top right* shows a schematic view of the surface of the SC, based on the work of McIlwain (1983), with approximate locations of the horizontal and vertical meridians of the eye (*HM* and *VM*, respectively). Recording sites for data plotted in **A-E** are shown by *filled dots* next to the labels (**A-E**). **A-E** Plots of the magnitude of the neuronal response during the first 200 ms after sound onset as a function of stimulus location and eye position. *Filled circles* Eye centered in the orbit (0±5°), *open squares* eye directed 10° to the right, *open inverted triangles* eye directed 10° to the left

the more effective unimodal stimulus (Stein and Meredith 1993). Cells showing significantly stronger responses to bimodal targets are said to show *response enhancement,* while cells showing significantly weaker responses to bimodal targets are said to show bimodal *response depression.* Only data obtained during periods when the cat's eyes were steady were used for these analyses.

When the eye was centered in the orbit, intersensory interactions were statistically significant in 27% of the cells tested (12/43 neurons). In 41 cells, the magnitude of intersensory interactions was tested at two or more eye positions. The vast majority of neurons showed similar bimodal interactions regardless of the position of the eyes in the orbit, as illustrated in Fig. 8.

The magnitude of bimodal interactions varied widely (range of +1563 to –70% in 43 neurons). We determined the sign of the interaction (enhancement or depression) for each neuron at different eye positions and found that 40 of the 41 cells (97%) showed the same sign of interaction (enhancement or depression) at all eye positions tested. We also determined whether the magnitude of response to bimodal stimuli was affected by eye position. In 36 of 40 neurons, the number of spikes evoked by bimodal stimuli did not change significantly across eye positions relative to the number of spikes evoked by the more effective unimodal stimulus. Thus, 10° changes in eye position did not produce a significant change in bimodal interactions in 90% of the neurons tested.

## Neuronal responses to visual targets

The lack of effect of eye position on bimodal interactions in the SC led us to re-examine the effects of eye position on responses to visual stimuli. Neurons were classified as responding to visual stimuli if their discharge was tightly coupled to the onset or offset of visual targets, independently of whether or not the cat made a saccade to that target.

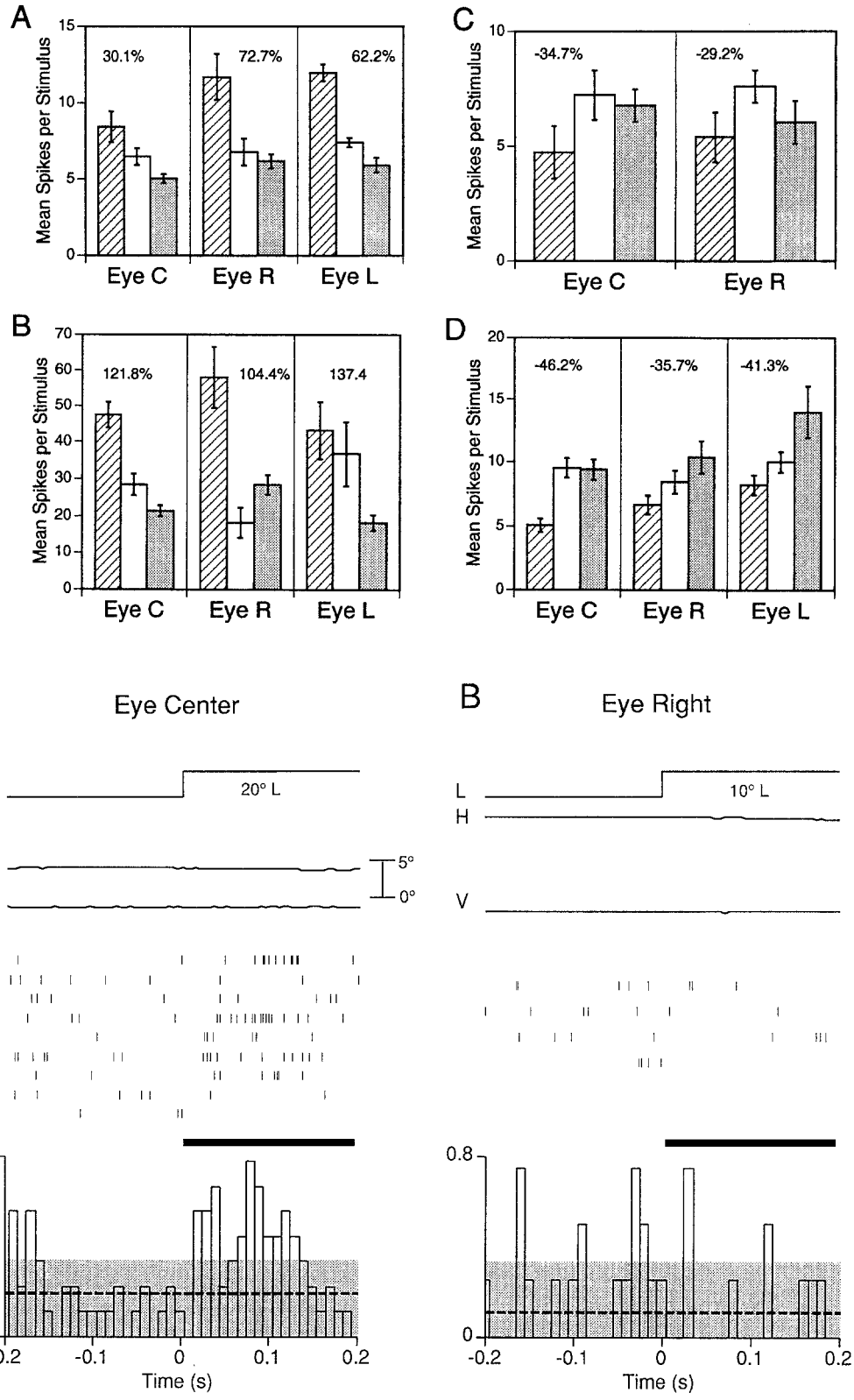


**Fig. 8A-D** Mean number of spikes evoked by stimulus onset or offset, as a function of target modality (*empty bars* light-emitting diode, *filled bars* speaker *hatched bars* both) and position of the eyes in the orbit for four SC neurons. **A, B** Bimodal enhancement of neuronal discharge for stimulus onset and offset. **C, D** Bimodal depression of neuronal discharge for stimulus onset and offset. *Error bars* ±1 SEM

**Fig. 9A,B** Effects of eye position on the responses of an intermediate-layer neuron to visual stimuli. The eyes remained immobile throughout the illustrated portion of these trials; *traces H and V* indicate the horizontal and vertical position of the eye throughout this portion of a typical trial; *calibration bar* applies to both **A** and **B**. Traces, rasters, and histograms are aligned on stimulus onset at 0 ms, as indicated by the stimulus trace (*L*) and by the *black bar* above the histograms. **A** Responses to LED onset when the eye was stationary and centered in the orbit (0±5°). Each *fine vertical bar* represents one action potential, and each *raster* represents the response of this cell on one trial. Each histogram sums the responses in the raster above. The *vertical scale* is mean number of spikes per 10-ms bin. The *horizontal dashed line* across the histogram indicates the mean number of spikes per bin for the baseline period of these trials and the *shaded area* represents ±1 SE of the mean number of spikes in the baseline time window. **B** Rasters and histograms for trials when the horizontal position of the eye was to the right of center (10±5°) at the time of stimulus presentation. Retinal locations of visual stimuli in **A** and **B** are matched

The effects of eye position on responses to visual stimuli were studied in 55 SC units. The retinal locations of their visual receptive fields were determined by subtracting the position of the eye in the orbit from the head-centered position of the visual stimulus. Figure 9 illustrates the response of one cell to visual targets with identical retinal coordinates when the eye was centered in the orbit and when it was directed 10° to the right. The number of spikes evoked by visual stimuli was significantly greater when the eye was near primary position than when it was directed to the right.

Regression techniques were used to separate the effects of receptive field location from the effects of eye position in the orbit. Multiple analysis of covariance showed that the visually evoked responses of one-third of the cells tested were significantly affected by the position of the eyes in the orbit, as shown in TableÊ2. In 19 of 55 neurons tested, there was a significant linear effect of horizontal eye position on the visually evoked response. The number of cells showing a significant effect of eye position was unaffected by whether an adjustment was made for background activity. Adding nonlinear components improved the degree of fit in only 2 neurons.

In order to determine whether these cells exhibited shifts in the optimal retinal location of visual stimuli, we plotted receptive field locations at different eye positions and found that these neurons did not show detectable shifts in the location of their receptive fields. The slopes of the best-fit linear regression equations relating horizontal eye position at the time of stimulus presentation to the number of spikes evoked by a visual stimulus ranged from 1.12 spikes/deg in the ipsilateral direction to 1.3 spikes/deg in the contralateral direction. Because the values of most slopes were relatively low, small changes in eye position would not greatly affect responses to visual targets at a given retinal location, but larger changes in eye position could noticeably modulate typical responses to visual stimuli, as shown in Fig. 9 for a 10° change in eye position.

The slopes of the best-fit linear regression equations were plotted as a function of the location of the recording site for all cells in which the coordinates of the recording site could be determined with sufficient accuracy. There was a significant positive relationship between location of the recording site and the strength of the effect of horizontal eye position. For 13 neurons recorded from the anterior half of the SC, the mean slope of the linear regression equation relating horizontal eye position to the number of spikes in the first 200 ms after LED onset was +0.280, where positive values indicate greater response when the eyes were directed ipsilaterally. In contrast, the mean slope for nine neurons recorded from the posterior half of the SC was –0.203, indicating that these neurons tended to respond more vigorously when the eyes were directed toward the contralateral visual field. The *proportion* of neurons with positive versus negative slopes was also significantly different for recording sites in the anterior SC and those in the posterior SC ($X^2$=4, two-tailed $P$=0.04). Because of the experimental apparatus and procedure, the range of vertical eye positions was too small to permit quantification.

## Discussion

Orienting movements of the eyes and head require transformations of sensory signals into motor commands which may not be in the coordinates of the sensory signals. In addition, different sensory pathways encode target location in different coordinates: the locations of visual targets are encoded from the retinal locus stimulated by the target, while sound location is computed from interaural differences in timing and intensity of auditory stimuli (Knudsen et al. 1987). In species with mobile pinnae, changes in pinna position alter these cues to sound location and thus auditory targets are localized head-pinnae-centered coordinates (Middlebrooks and Knudsen 1987). Our results indicate that the vast majority of sound-sensitive neurons in cat SC exhibit significant shifts in the optimal location of auditory stimuli with changes in eye position. These neurons cannot represent the location of sounds in head-pinna coordinates. However, because the population of neurons did not compensate completely for changes in eye position, head-centered maps may coexist with an eye-centered map in the SC. Groh and Sparks (1992) have recently proposed two models for computing eye-centered auditory signals from head-centered signals. Suitable manipulations of these models would permit neural circuits to generate signals in head-centered, eye-centered, and intermediate coordinates.

### Saccades to auditory targets

Saccadic errors to auditory, visual, and bimodal targets were comparable, indicating that cats are capable of making saccades to sounds with reasonable accuracy. Because we did not require highly accurate saccades, the ability of cats to program accurate saccades toward sound sources may be considerably greater than our data indicate.

Saccades to visual, auditory, and bimodal targets showed similar patterns of error as a function of target location. Moreover, all the cats showed at least partial compensation for initial eye position in making saccades to auditory targets. It is somewhat more surprising that these cats also showed only partial compensation for the initial position of the eye in computing the amplitude and direction of saccades to visual and bimodal targets. Previous work in other species suggests that saccades to sounds may differ from saccades to visual targets in their timing: While the latency of saccades to visual targets increases as target eccentricity increases, the latency of saccades to auditory targets decreases with target eccentricity. In addition, the velocity of saccades to auditory targets is less than the velocity of saccades to visual targets (Jay and Sparks 1989).

Neuronal responses to auditory stimuli

Most neurons which responded to auditory stimuli also responded to visual stimuli, as has often been shown. In previous studies, latencies of SC neurons to visual targets have been found to vary over a range of about 35 ms (55–57 ms in cat, Guitton and Munoz 1991; 76.1 ms in macaque, Jay and Sparks 1987; and 82.5 ms in cat, Meredith et al. 1987). Significantly lower values for responses to auditory targets have been reported: as low as 12.9 ms for auditory targets at least 20 dB above threshold in cat (Hirsch et al. 1985). Several other studies also indicate that sound-responsive SC neurons have latencies of less than 20 ms for the first spike following presentation of an auditory stimulus (e.g., Meredith et al. 1987). Although our median response latency to auditory targets, 50 ms, is considerably longer than these values, it is quite close to the mean value (44.5 ms) reported by Jay and Sparks in the macaque. It is possible that cortical circuits gate off shorter-latency auditory responses in alert animals and that the shorter latencies seen in anesthetized cats reflect the absence of this gating, but it is also possible that procedural variations – including the intensity of the stimuli, the method for calculating latency, and the use of anesthetic and paralytic agents – account for some of the difference in latency in alert and anesthetized animals.

*The coordinates of auditory signals in the superior colliculus*

The map of auditory space in the tectum must be constructed by the central nervous system from the time and intensity of sound waves at the two ears (e.g., Knudsen et al. 1987). Shifts in the position of the pinnae of cats result in corresponding shifts in the location of auditory receptive fields in the SC (Middlebrooks and Knudsen 1987), and, therefore, cats must combine information on the current position of the head and pinnae with interaural cues to localize sound sources. The idea that the behaving animal must also compensate for the position of the eyes in the orbit, originally suggested by the work of Jay and Sparks (1987) in macaques, has appeared to conflict with a previous study in the cat (Harris et al. 1980). However, the present results are remarkably similar to those of Jay and Sparks. Similar findings by Hartline and colleagues (1989) are also consistent with the hypothesis that there are shifts in the location of the population of sound-responsive neurons in the SC when cats redirect their eyes. Because all of our data were obtained with the eyes steady and with the head fixed securely, our results do not reflect dynamic changes associated with saccades, nor do they indicate how the nervous system deals with independent changes in the position of the head, eyes, and pinnae.

Our procedures almost certainly lead to an underestimation of the percentage of SC neurons in which sound-evoked activity is affected by the position of the eyes in the orbit. If we had used a greater range of eye positions and been able to obtain more data from each neuron, we would almost certainly have found significant effects of eye position in a larger fraction of our sample. Our measure of%S estimated the change in the center of the auditory receptive field as a function of eye position. On average, sound-responsive neurons showed a shift of 62.1%. This value is comparable with the mean value of 54% shift in the borders of auditory receptive fields found by Jay and Sparks in the macaque. The data of the two studies seem to indicate a substantial but incomplete transformation of auditory signals from head- to eye-centered coordinates.

Some of the cells tested in the present study showed significant increases in their responses to sounds at most of the speaker locations tested when the eyes were in certain orbital positions. This pattern, which we quantified as%F, averaged 25.3%, suggesting that there may also be expansion of auditory receptive fields when the eyes are directed eccentrically, leading to activation of a larger population of sound-sensitive neurons with eccentric eye positions than when the eyes are centered in the orbit.

Some sound-responsive neurons were not significantly affected by eye position. A few neurons of this type were also reported by Jay and Sparks in the macaque, and it is possible that such cells encode the position of the speaker with respect to the head (Harris et al. 1980).

*Sources of head-centered auditory signals*

Of several potential sources of auditory input to the SC, the inferior colliculus (IC) and the auditory-recipient cortex in the anterior ectosylvian sulcus (AES) seem most likely to provide binaural signals. AES neurons have been shown to be sensitive to the spatial locations of sounds (Korte and Rauschecker 1993; Middlebrooks et al. 1994). Auditory responses of IC neurons have also been studied. Most investigators have used barbiturate anesthesia, which has potent depressant effects, presumably mediated by GABAergic mechanisms (Kuwada et al. 1987). There seems to be a population of IC neurons, particularly in the central nucleus of IC, selective for the azimuthal location of sounds (Aitkin et al. 1985; Calford et al. 1986). Although peripheral factors may account for the selectivity of some of these neurons, particularly with stimuli of relatively low intensity (Semple et al. 1983), the responses of the majority of azimuth-selective neurons appear to reflect central processing of binaural information. Jay and Sparks (1987) also recorded from a few IC neurons in alert monkeys; the five cells studied showed some selectivity for the head-centered location of sounds. Their response latencies were also much shorter than those of SC neurons to the same stimuli, suggesting that the IC may not be the sole direct source of head-centered auditory signals to the SC.

*Implications of mobile auditory receptive fields*

Although we have described the effects of eye position on SC neurons, we do not know the mechanisms in-

volved in producing such shifts. Two neurally plausible models for producing these shifts have been proposed (Groh and Sparks 1992). Manipulations of these models by associative processes and by changes in synaptic function produce changes in the extent of the shift within identical neuronal networks.

In young barn owls, the role of vision in calibrating neural maps of sound location has been well established (Knudsen and Knudsen 1990), and similar processes may occur in young mammals (King and Moore 1991). It is not clear whether such processes could be involved in the shifts of auditory receptive field location with eye position in adults, but associative or Hebbian synaptic mechanisms could certainly be used to establish synaptic efficacy in the neural networks involved in transforming head-centered auditory signals into eye-centered signals (Groh and Sparks 1992).

While presentation of coincident bimodal sensory stimuli (visual and auditory signals at the same location in space) enhances the probability of detecting targets and producing overt orienting behavior (Reuter-Lorenz et al. 1992; Stein et al. 1988), presentation of spatially disparate visual and auditory stimuli reduces the probability of correct behavioral orientation (Kurylo et al. 1992; Stein et al. 1988). Because the visual and auditory receptive fields of SC neurons are generally large, small displacements of the eyes might be expected to have relatively little effect on the alignment of visual and auditory maps. However, our data indicate that displacements of 10° substantially affect the magnitude of response to auditory stimuli. Simultaneous bimodal stimuli can also enhance premotor activity of SC neurons (Peck 1987), an outcome which would be unlikely if movements of the eyes, head, and pinnae automatically displaced modality-specific receptive fields.

## Neuronal responses to bimodal targets

In a variety of species, neurons in the deeper tectal layers exhibit bimodal interactions (Stein and Meredith 1993): Some neurons exhibit enhancement of their responses when simultaneous bimodal stimuli are presented, while others show depression of response when simultaneous bimodal stimuli are presented. In this paper, we extend those observations to situations in which voluntary movements of the eyes have displaced retinal coordinates relative to head-centered coordinates.

Most of our cells showed relatively modest enhancement or depression of neuronal discharge to bimodal stimulation, and less than one-quarter showed interactions which were too large to be the result of simple additive effects of their unimodal inputs. Multisensory interactions are most likely to be multiplicative when low-intensity stimuli are used, and the degree of bimodal interaction decreases as stimulus intensity increases (Stein and Meredith 1993). Because moderately intense sensory stimuli were used for the behavioral tasks, we expect that the percentage of cells showing bimodal interactions would be greater if we used less intense stimuli.

Almost all SC neurons whose axons project through the tecto-recticulo-spinal tract are multisensory. Such neurons may form an integrated multisensory network as well as provide access to neuronal circuits mediating orienting behavior. As noted above, multisensory stimuli also influence the probability of overt orienting responses (Stein et al. 1988). The results of the present study indicate that different sensory inputs remain integrated within the SC even when the eyes are directed eccentrically by up to 10°. Although the cat's oculomotor range is greater than 20°, we generally did not collect enough data for trials with more eccentric eye positions to assess whether response depression would have been more prevalent if the eyes were directed more eccentrically. However, because 10° displacements produced significant shifts in the most effective locus of auditory stimuli for the majority of sound-sensitive neurons, it seems reasonable to expect that the same degree of displacement would influence multisensory integration insofar as such integration depends on the passive alignment of receptive fields.

## Neuronal responses to visual targets

In earlier work on the SC of alert cats, Peck and colleagues (1980) reported that the visual responses of some cells in the caudal SC were gated by the position of the eye in the orbit, while those in the anterior third appeared to be unaffected by eye position. In the present study, we analyzed the effect of horizontal eye position on cells recorded throughout the rostrocaudal extent of the SC, expecting that statistically significant effects of eye position would be rare among cells recorded rostrally. However, we found that the effects of eye position were graded in magnitude across the rostrocaudal extent of the SC.

There are three possible interpretations for the effects of eye position on the response of the SC neurons to visual stimuli. First, the location of the population of active neurons might shift with eye position. This seems unlikely, because we did not detect shifts in receptive field location as a function of eye position. Rather, these cells had visual receptive fields which were in retinocentric coordinates. None of them responded to the *spatial location* of visual targets, independent of the position of the eyes in the orbit. These results are consistent with the findings of other investigators. In contrast, some neurons in the frontal cortex seem to be activated by visual stimuli in a particular region of egocentric or head-centered space, independent of their retinotopic location (e.g., Gentilucci et al. 1983).

Second, individual neurons throughout the active population could be gated by the position of the eyes in the orbit, and the overall the magnitude of the response throughout the population might increase as the eyes are directed to certain locations in the orbit. Recent studies by Andersen and colleagues (1990) have shown that the visual receptive fields of neurons in areas 7A and in the

lateral intraparietal area (LIP) of the posterior parietal cortex of the macaque are retinotopically organized, and that the magnitude of the response of parietal neurons to visual stimuli is gated by eye position. Similar modulation of visual responses by eye position seems to be widespread in the visual system, having been observed in a variety of cortical areas (e.g., Funahashi et al. 1990; Weyand and Malpeli 1993) and in visual-recipient portions of the thalamus (Schlag et al. 1980; Lal and Friedlander 1990; Robinson et al. 1990).

The third possibility is that the size of the population of neurons recruited by a visual stimulus at a given receptive field location could increase as a function of eye position. Impending saccades seem to shift visual receptive fields of neurons in both the lateral intraparietal cortex (Duhamel et al. 1992) and the SC (Walker and Goldberg 1992). Although these results have been interpreted as a predictive remapping of the visual representation in this area, published data are also consistent with an expansion of visual receptive fields prior to saccadic eye movements. Grasse et al. (1993) have reported increases in the size of visual receptive fields of neurons in the superficial layers of the SC by intravenous administration of amphetamine, although the sources of the extraretinal signals producing this modulation are unknown.

It has been suggested that the central nervous system combines eye position and retinotopic signals to construct information about the position of visual targets in space (e.g., Andersen et al. 1990). Weyand and Malpeli (1993) have recently reported that eye position exerts a significant influence on visual excitability in a sizable fraction of neurons in striate cortex, and their results are compatible with a cortical origin for the effects of eye position on visual processing in the SC. Constructing a head-centered frame of reference requires only that cells with similar retinotopic information have different sensitivities to eye position, not that such cells be sharply tuned for eye position. However, if populations of SC neurons are involved in such computations, then it is far from clear why a substantial proportion of SC neurons should participate in computing the eye-centered positions of auditory stimuli from head-centered input signals. Similar considerations have led to models that incorporate eye-centered signals from the SC as the input to brain stem circuits that generate saccades.

**Acknowledgements** Supported by the US Public Health Service (NS-21238). We thank Diann Allee Prescott for exemplary animal care and assistance with surgery, Franklin Wartman for help with the earlier experiments, and Li-Jing Yao for assistance in making the figures.

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