Effect of eye position on saccades and neuronal responses to acoustic stimuli in the superior colliculus of the behaving cat

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Running Head: Motor error in the cat superior colliculus

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ABSTRACT

We examined the motor error hypothesis of visual and auditory interaction in the superior colliculus (SC), first tested by Jay and Sparks (J Neurophysiol 57: 35-55, 1987) in the monkey. We trained cats to direct their eyes to the location of acoustic sources and studied the effects of eye position on both the ability of cats to localize sounds and the auditory responses of SC neurons to similar sounds with the head restrained. Sound localization accuracy was generally not affected by initial eye position, i.e. accuracy was not proportionally affected by the deviation of the eyes from the primary position at the time of stimulus presentation, demonstrating that eye position is taken into account when orienting to acoustic targets. The responses of most single SC neurons to acoustic stimuli in the intact cat were modulated by eye position in the direction consistent with the predictions of the ‘motor error’ hypothesis (Sparks, 1986; Physiol Rev 66: 118-171), but the shift accounted for only 2/3 of the initial deviation of the eyes. However, when the average horizontal sound localization error, which was ~35 % of the target amplitude, was taken into account, the magnitude of the horizontal shifts in the SC auditory receptive fields matched the observed behavior. The modulation by eye position was not due to concomitant movements of the external ears, as confirmed by recordings carried out after immobilizing the pinnae of one cat. However, the pattern of modulation after pinnae immobilization was inconsistent with the observations in the intact cat, suggesting that in the intact animal information about the position of the pinnae may be taken into account.
INTRODUCTION

In anesthetized animals the various sensory and motor maps in the superior colliculus (SC) are in approximate alignment (Gordon, 1973; King and Palmer, 1983; Meredith and Stein, 1985; Stein and Meredith, 1993, Middlebrooks and Knudsen, 1984; Stein and Clamann, 1981) meaning that acoustic and visual stimuli at the same spatial locations stimulate the same part of the SC. The alignment of auditory and visual topography is thought to provide a substrate for sensorimotor integration (Harris et al., 1980; Stein and Meredith, 1993). However, as first pointed out by Pöppel (1973), since the coordinate systems for vision and audition are different, with the visual map oculocentric and the auditory map head-centered, this alignment holds only when the two coordinate systems are aligned, i.e., when the eyes and head point in the same direction.

Thus, in behaving animals, whose eyes are free to move in the head, one would expect the SC maps to become misaligned whenever the animal is not looking straight ahead. If this alignment is critical for sound localization or for bimodal integration, then the consequence of misalignment between these two maps might be mislocalization of the source of a sound whenever the eyes are away from the primary position. Furthermore, the magnitude of the expected error in sound localization should be proportional to the deviation of the eyes from the primary position (Harris et al., 1980). This hypothesis can be tested behaviorally.

Alternatively, the collicular representation of auditory space could shift to compensate for changes in eye position to maintain the alignment of the receptive fields (RFs) across the different modalities. Such a shift would require a modulating signal proportional to the position of the eyes within the orbit, in order to yield a representation of the eye motor error, which is the difference between eye position and the target. In this scheme, also known as the ‘motor error hypothesis’ (Sparks, 1986), the shifted auditory RFs would not encode the location of auditory sources relative to the head, but rather their location relative to the position of the eyes within the orbit. This hypothesis can be tested physiologically.

Jay and Sparks (1987) found evidence supporting the motor error hypothesis in the SC of the monkey: they found that the auditory response was modulated by eye position though it only partly compensated for the motor error. More recently Groh et al. (2001) and Zwiets et al., (2004) both found evidence of modulation by eye position in auditory responses by a variable number of cells in the inferior colliculus even though their monkeys were not trained to orient to the acoustic stimuli. However, in the cat conflicting evidence has been presented. Harris et al. (1980) claim that cats do not move their eyes enough to require compensation while Hartline et al. (1995) and Peck et al. (1995) provide evidence for compensation. Furthermore, shifts of auditory receptive fields in the SC of cats could result from changes in the acoustic input to the eardrums brought about by the highly mobile pinnae (Middlebrooks and Knudsen, 1987). However, the interpretation of the available data in all three studies (Harris et al., 1980; Hartline et al., 1995; Peck et al., 1995) is hindered by limited sample size, untrained and inconsistent subjects, and inadequate monitoring of eye or ear position. We have designed this study to overcome these problems by using cats trained to localize sound by looking at the acoustic sources and well-controlled experimental conditions.

Our results show that most cells driven by acoustic stimuli in the deep and intermediate layers of the superior colliculus of the cat are modulated by eye position in a manner consonant with the motor error hypothesis. Although the shift in auditory receptive fields did not compensate fully for the motor error, it did match the behavioral motor error, which was calculated on the basis of the propensity for the saccades to auditory targets to undershoot the
target. Finally, by recording from cells in the SC in a cat whose pinnae had been immobilized, we showed for the first time that the modulation cannot be due to the changes in acoustics brought about by movements of the pinnae of the cat while fixating different positions. However, the modulation seen in the pinna immobilized cat was not consistent with the modulation seen in the intact cat, suggesting that eye position, pinna position and a motor efferent copy command may all play a role in the acoustic modulation in the SC. A preliminary account of portions of this work have been presented (Populin and Yin, 1998a).
MATERIALS AND METHODS

Subjects, Surgery, and Experimental Setup

A detailed description of the materials, methods, and animal training procedures has been presented previously (Populin and Yin, 1998b). Briefly, ten cats were trained to localize sound by looking at the perceived location of the sources. Single neuronal recordings made in the SC of six of them are included in this report. Under sterile conditions a recording cylinder was implanted on the midline of the skull to access the SC on both sides with vertically-oriented electrode penetrations. The animals had already undergone a surgical procedure to implant eye (Judge et al., 1980) and pinna (Populin and Yin, 1998c) coils, and a post to restrain the head, and had been trained on the behavioral task.

Anesthesia was first induced with an intramuscular injection of Ketamine (20 mg/kg) and Acepromazine (0.2 mg/kg), followed by intravenous sodium pentobarbital, or gas (halothane or isoflurane). All surgical and experimental procedures employed were approved by the University of Wisconsin Animal Care Committee and were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals.

The experiments were carried out in a dimly illuminated (2.2 x 2.5 x 2.5 m) single-walled sound attenuated chamber with the inner walls and major pieces of equipment in it covered with 10.2 cm Sonex foam (Ilbruck, Minneapolis, MN) to attenuate acoustic reflections. All experiments were carried out under head restrained conditions.

Eye and pinna movement recordings and stimuli presentation

Eye and pinna movements were recorded with the scleral search coil technique (Robinson, 1963). The analog output of the CNC Engineering (Seattle, WA) system used to measure eye and pinna movements was digitally sampled at 500 Hz with an A/D converter and stored on disk for off-line analysis.

Acoustic stimuli were generated with a Digital Stimulus System (Rhode, 1976) and presented via Radio Shack Super tweeters (model 40-1310A) that had been modified to transduce low frequencies. Visual stimuli were presented from small (2.0 mm-dia.) red ($\lambda_{\text{max}} = 635 \text{ nm}$) light emitting diodes (LEDs) that subtended a visual angle of 0.2$^\circ$ and were mounted at the center of each speaker. The transducers were placed in the frontal hemifield, 62 cm away from the cat’s head behind a dark curtain that allowed sounds to be heard and LEDs to be seen when lit. The standard acoustic stimulus was a 163-msec noise burst (0.1-25 kHz) with 7 msec rise-fall windows, and was repeated as needed to produce bursts of longer durations. All aspects of data acquisition and stimulus presentation were controlled by a MicroVAX II minicomputer (Digital Equipment Co, Maynard, MA) running custom software.

Physiological Recordings

Recording sessions started five to seven days after the implantation of the recording cylinder, took place five to six times a week, and lasted about 3 hours each. The animals were continuously monitored through closed circuit TV for signs of distress. The end of a recording session was typically signaled by the animal falling asleep, or stopping work due to satiety.

Parylene covered tungsten microelectrodes (Micro Probe Inc, Potomac, MD) were driven through the intact dura mater with an eccentric Narishige (Narishige International USA, INC, East Meadow, NY) microdrive. Extracellular signals were amplified and bandpass filtered (300-3000 Hz). A window discriminator (Bak Electronics, Mount Airy, MD) was used to generate pulses every time an action potential met the spatial and temporal criteria set by the investigator.
These were recorded with 1 μsec resolution with a custom-made event timer. All data presented in this report are from well-isolated single neurons.

Behavioral Tasks

We initially trained the cats on a variety of visual and auditory oculomotor tasks (visual and auditory fixations, standard and delayed saccades, and sensory probes, as described in Populin and Yin, 1998b) delivered in random order so that on any given trial the cat could not predict what the task would be. This training period took an average of seven months, at the end of which we did a sterile surgery and mounted a recording cylinder on the cat to commence physiological recordings from the SC.

The behavioral experiments presented below used the auditory standard saccade task (Fig. 1A). This task used a visual fixation stimulus (LED), which allowed us to control the initial position of the eyes, and an acoustic stimulus (SPEAKER), which was the target for the saccade. The cat was required to first acquire and maintain fixation on the fixation LED until it was turned off at the same time that the speaker was turned on, and then make a saccade to the newly presented target and maintain fixation until the sound was turned off. A reward was delivered if temporal and spatial criteria were met. The rationale for establishing the spatial criteria for success is discussed in Populin and Yin (1998b).

During physiological recordings to determine if the responses of SC auditory neurons were modulated by fixation position, we used the auditory sensory probe task (Fig. 1B). This task is a variation of the auditory delayed saccade task (Populin and Yin, 1998b), which was used for training because it required the cats to treat acoustic stimuli as targets for saccadic eye movements. In the sensory probe task the cat is required to fixate for a predetermined period of time on one of 3-5 fixation LEDs located along the horizontal axis. During this period of fixation a broadband noise burst (probe SPEAKER), presented from another speaker was used to probe the neuron’s responses to the sound. To receive a food reward the cat had to maintain its eyes within an electronic window, typically ≤ (6° x 6°), centered about the fixation LED until the end of the trial when both the fixation LED and probe speaker were turned off. Usually we varied one or more parameters (e.g. the fixation LED or the acoustic speaker location) during any particular recording session so that a variety of tasks was always presented so the cat could never anticipate what the upcoming trial would be.

For the auditory delayed saccade task (not shown) which was used in training, the fixation LED was turned off after a 300-500 msec delay, which signaled the cat to make a saccade to the speaker. It is important to note that the sensory probe and delayed saccade tasks are identical up to the time that the fixation LED is extinguished to signal the saccade. Ideally, we would have preferred to use the delayed saccade task for our recordings, but the best response area of most units was outside the oculomotor range of the cat, which is approximately ±20°. We are confident that the cat considered the probe speakers as potential saccade targets because when we switched to runs with auditory delayed saccades or auditory fixation tasks, they immediately made short-latency saccades to those targets.

Pinnae immobilization

Our behavioral studies showed that cats move their external ears in a systematic fashion in response to acoustic stimuli and when fixating at different spatial positions (Populin and Yin, 1998c). Therefore, the position of the ears varies as the eye position changes. To control for changes in the acoustic input to the eardrums brought about by the moving pinnae, we
immobilized them for a final set of physiological recordings in one cat. We would have preferred to immobilize them reversibly by anesthetizing the branches of the facial nerve while holding a single neuron but this proved too difficult. We also tried taping the pinnae but this was unsuccessful in holding the pinnae steady. Finally we resorted to acutely denervating the pinnae. Under sterile conditions we cut the auriculoposterior and temporal branches of the facial nerve that innervate the caudal and rostral pinna musculature, respectively. This procedure was successful in immobilizing the pinnae for about 3 or 4 weeks until the nerves regenerated and presumably also deafferented the pinnae so that the proprioceptive signals were also severed.

Data Analysis

In the psychophysical experiments, the dependent variable of interest was final eye position after saccadic eye movements to the acoustic targets. A criterion based on the variability of the velocity of the eyes during steady fixation was used to mark the start and end of an eye movement (Populin and Yin, 1998b). Briefly, the end of and return to fixation were determined by the time at which the amplitude of the velocity function exceeded and returned to within two standard deviations of the mean baseline velocity, respectively. The mean velocity baseline was computed from 100 msec prior to 30 msec after target onset, a period during which the eyes were expected to be stationary. The eye position at the time of the return to fixation was considered to be the final eye position for a saccade. If corrective eye movements took place before the reward or within 500 msec after the end of fixation, the return to fixation measurement was carried out after the completion of the last movement.

Dot rasters and histograms were constructed to qualitatively evaluate neuronal responses. For quantitative evaluation the mean number of action potentials per trial occurring within a predefined window was determined. For most neurons a 500 msec window, starting 5 msec after the onset of the acoustic stimulus, was used. The auditory RF of a SC neuron is operationally defined as the area of space within which a stimulus evokes a response.

Because our primary concern was the role of eye position on the responses of SC neurons to acoustic stimuli, we usually began by studying the responses of the neurons to a probe from a single fixed position while varying the eye position using the sensory probe task. To determine if auditory responses were modulated by fixation position, 95% confidence intervals were computed for the mean response from each fixation position. The auditory responses of a neuron were classified as modulated by fixation position if one pair of responses to different fixation positions was significantly different (p < 0.05). The exact shape of the resulting functions relating neural responses to fixation position is determined by the horizontal position of the speaker selected for studying the neuron, the shape of the RFs, and the way the RFs are modulated by fixation position.

When stable recording conditions and a cooperating animal coincided, a more complete representation of the neuron’s RF was obtained by recording the responses evoked from sounds presented from different speakers along the horizontal axis for three to five different fixation positions. The data were plotted both as a function of the location of the speakers relative to the animal’s head, and as a function of the distance between the fixation point and the speakers (i.e., the motor error). The extent to which the RF functions obtained for the different fixation conditions shifted and became aligned or misaligned because of the change in coordinates constituted the test of the motor error hypothesis.

We computed the shift in azimuth of the RFs that resulted from two different eye positions relative to the eyes-centered condition as follows. For example, for each data point from the RFs
measured when the cat fixated to the left we measured how much that point was shifted in azimuth relative to the RF when the eyes were fixating straight ahead. This was done by computing at each data point the difference in azimuth at corresponding discharge rates, as illustrated by the dashed arrow in Figure 2. This process was repeated using the data points from the RF obtained when the cat fixated at the center, as indicated by the solid horizontal arrow in Figure 2. When the azimuth at which the line intersected the RF fell between data points, the azimuth of intersection was determined using linear interpolation. Shifts to the right of the center RF were positive while shifts to the left were negative. These differences in azimuth were then averaged. When measuring the differences, care was taken to respect the shapes of the RFs; for example, when RFs exhibited a ‘peak’ response, the difference in azimuth took into account the medial and the lateral portions of the RFs in order to obtain a true estimate of the shift in the RFs. Neurons with RFs that were complex with many peaks and dips were not included. A motor error index (MEI) was computed by taking the ratio of the computed shift in the RFs and the size and direction of the shift in eye position. When the RFs exhibited a ‘peak’ type profile, characterized by responses on either side of the peak that fell by 20% or more, an MEI was computed also for the medial edge of the RF only; this analysis is comparable to that performed by Jay and Sparks (1987). An MEI of 1.0 resulted if the RF shifted in the same direction and with the same magnitude as the shift in eye position. This process was repeated for RFs recorded with fixation to the right. For each neuron, we plotted the MEI for leftward fixations against the MEI for rightward fixations. Data points that fell in the upper right-hand quadrant were, therefore, consistent with the motor error hypothesis, with perfect motor error for points at (1, 1).

**Histology**

After completion of the experiments the cats were anesthetized with an intra-muscular injection of Ketamine and Acepromazine, and 2-3 pins were placed in the brain with the recording microdrive at known positions within the recording chamber, rostrally and caudally to the recording area, and in parallel to the electrode penetrations. Figure 3 shows Cat6’s midbrain with one pin inserted caudally to the left SC, and another pin inserted rostrally to the right SC. The hash patterns overlaying each SC represent the approximate areas in which electrode penetrations were made in relation to the location of the pins.

After placing the pins, a lethal dose of sodium pentobarbital (150 mg) was given intravenously, followed by perfusion through the heart with physiological saline and (10 %) formalin. The brains were removed from the skull and stored in 30% sucrose at 4°C for 24-48 hours. The midbrain was blocked using the pins as reference, frozen, cut into 50 μm sections in the coronal plane, and stained with cresyl violet. Individual penetrations were difficult to identify due to the long tenure of our cats, but numerous tracts traversing the SC could be observed. Camera lucida drawings and positional information referenced to the pins were used to confirm that the electrode penetrations reached the SC.
RESULTS

Effects of fixation position on sound localization accuracy

The first consideration was to determine whether Pöppel’s (1973) paradox was behaviorally relevant, i.e., whether there was any effect of initial eye position on sound localization accuracy. To address this question we used the auditory standard-saccade task (Populin and Yin, 1998b) with different initial fixation points (LED in Fig. 1A) and broadband noise stimuli as acoustic targets. Trials of this type were randomly intermixed among different types of visual and acoustic trials to numerous other targets (Populin and Yin, 1998b). Figure 4 illustrates eye movements to an acoustic target at (0º, 24º) recorded under those conditions. The cat was required to fixate LEDs at (±4º, 0º) for 1000 msec or an LED at (0º, 0º) for 500 msec. The dots that form each trace represent digital samples of the analog output of the eye coil system. In approximately 90% of trials involving acoustic trials on the horizontal plane cats oriented with a single saccadic eye movement; for acoustic targets on the vertical plane, approximately 95% of trials were completed with a single saccade. The slope of the main sequence computed from these eye movements was consistent with those measured in our previous work (Populin and Yin, 1999).

Data from six cats with different levels of experience were analyzed to address this question. The trajectories of eye movements recorded in successful trials initiated from different fixation positions are plotted in Figure 5A-F. For the experiment shown in Figure 5A the acoustic target was located at (18º, 13.5º) and the starting fixation positions were at (±9º, 0º) and (0º, 0º). Cat C9 was a novice subject, and the data were collected in the 8th behavioral session; the animal had not been exposed to this acoustic target until this session. As is typical of cats in head-restrained conditions (Populin and Yin, 1998b), subject C9 undershot the acoustic target. Although the trajectories of the eye movements were different in the three fixation conditions, the eye movements ended up in roughly the same spatial location. The eyes took the most direct path when the fixation LED was on the same side of the target (9º, 0º), and the most curved when the fixation LED was on the opposite side (-9º, 0º).

The acoustic targets for the experiment shown in Figure 5B were at (0º, -22º) and (0º, 24º) with fixation positions at (±3.5º, 0º) and (0º, 0º). Cat G1 was an experienced subject; these data, a subset of which is shown in Figure 4, were collected in the 292nd behavioral session. This subject was very accurate in localizing sound sources regardless of initial eye position, and her data reveal no effect of initial eye position on sound localization.

The data shown in Figure 5C are from subject C5 11th experimental session. The acoustic target was located at (8º, 13.5º). This was the first session in which subject C5 was presented with this acoustic target. The trajectories of the eye movements were similar to those of subject C9 in Figure 5A. Though they show more corrections than the other subjects, they were consistently aimed at the target.

For the experiments in Figure 5D and 5E the acoustic target was located at (-18º, 0º) and the initial starting positions at (±9º, 0º) and (0º, 0º). Subjects C6 and C14 were well practiced at the time of the recordings, 81-83rd and 159-163rd behavioral sessions, respectively. Both subjects mislocalized this acoustic target, although with different types of errors: while subject C6 localized the target below the horizontal plane, subject C14 localized it above. Interestingly, the pattern of errors made by each subject was consistent across the three experimental conditions.

Lastly, the data shown in Figure 5F are from subject G7 and were collected in the 55-60th behavioral sessions. The acoustic target was placed at (0º, 24º) and the starting points at (±6º, 0º) and (0º, 0º). Unlike the previous subjects G7 exhibited a clear bias in its final eye position,
which is indicative of incomplete compensation for the initial position of the eyes along the horizontal plane.

Figure 6 summarizes localization performance from the subjects presented in Figure 5; data from some additional targets are included. In each panel the position of acoustic targets is plotted with an asterisk, the starting fixation positions are plotted with filled symbols and the corresponding mean final eye positions are plotted with open symbols of the same shape. Error bars represent 95% confidence intervals computed for the X and Y-axes separately. All trials, successful and unsuccessful, were included in the analysis.

There was no effect of initial eye position on the accuracy with which subjects C9, G1, and C5 (Fig. 6A, B, and C) localized the acoustic targets. The 95% confidence intervals computed for each of the mean final eye positions overlapped indicating that they were statistically indistinguishable. Similar observations were made for targets at other positions.

Subjects C6 and C14’s localization of an acoustic target at (-18º, 0º) showed an effect of eye position, as revealed by the non-overlapping 95% confidence intervals computed for each of the three mean final eye positions. Subject C6’s data (Fig. 6D) show a significant effect of eye position for the target at (-18º, 0º) only. The magnitude and sign of the mean error for the eye movements initiated from the primary position (0º, 0º), compared to those starting from fixation position to the right (9º, 0º), but not to the left, of the midline are nearly proportional to their initial separation. There was no effect of initial eye position on the localization of other acoustic targets such as those located above (0º, 9º) and to the right (18º, 0º) of the primary position.

Subject C14 (Fig. 6E) made large, yet consistent, localization errors on both the horizontal and vertical components in all three conditions. However, the differences among the three mean final eye positions cannot be predicted based on the initial fixation position. Specifically, the final eye position for the (±9º, 0º) starting fixation points were not significantly different. Furthermore, the localization error was smaller in the (9º, 0º) than in the (0º, 0º) fixation condition, which is the opposite of what one would expect if initial eye position was not taken into account to perform the eye movements to the acoustic target. Subject G7 (Fig. 6F) also showed a mixed pattern, that is an effect of initial eye position for some targets, those located along the vertical axis, but not an effect of initial eye position for others, those located along the horizontal axis.

Thus, for the six cats tested, only one of them showed a consistent mislocalization that was related to initial eye position. The accuracy of saccades to auditory targets of three of the cats was unrelated to initial eye position and for two cats there was a small but inconsistent effect. On average the mean horizontal localization error computed from 267 trials from four cats, across three different initial eye position, for targets with large horizontal component, was an undershoot of 35%.

Effects of fixation position on single SC neuron responses

General observations

As a microelectrode approached the SC from above, a predictable pattern of active and quiet areas was found in most penetrations. In cortex we encountered visually driven activity and below the quiet of the superior cistern, which indicated that the SC was near. The signature of the superficial layers of the SC was intense neural activity that changed in rate as the cat moved its eyes or visual stimuli were swept across the screen in front of the cat. The onset of this pattern was abrupt, and in marked contrast with the lack of activity just above. The area with this type of activity extended dorso-ventrally about 1.5 mm. The position of the tip of the
electrode within the visual map of the SC (Feldon et al., 1970) was inferred from the responses evoked by stimulating discrete areas of the contralateral visual field with a visual stimulus while the cat fixated an LED at the primary position (0°, 0°). We did not attempt to isolate neurons in the superficial layers of the SC. We searched for neurons that responded to acoustic stimuli as we lowered the electrode into the intermediate layers of the SC using a mixture of trials with visual and acoustic stimuli. In the caudal SC auditory neurons were typically found between 1.5-3.5 mm ventral to the top of the superficial layers, but in approaching the rostral SC the layer containing auditory neurons became progressively thinner (< 0.5 mm), with fewer auditory neurons.

Upon isolating a neuron responsive to sound we determined the stimulus position (from our available target locations) from which the strongest response could be evoked as well as the approximate threshold. The most sensitive speaker position was selected and the level of the stimulus was set at approximately 20 dB above threshold. Our first priority was to determine if the responses of the neuron using the sensory probe task, evoked from the most effective source location, were modulated by eye position. In cases in which we were able to maintain the recording for a prolonged period we characterized other parts of the neuron’s RF along the horizontal axis. As reported previously (Populin and Yin, 2002) the responses of most SC auditory neurons to identical acoustic stimuli were smaller in the sensory probe task compared to the auditory fixation task. In some cases the effect was so strong that there was virtually no response to the sensory probe. In any case, however, this condition most closely approximates the conditions used for the psychophysical studies.

With few exceptions, the 143 SC auditory neurons in our sample responded to broadband noise stimuli presented from sources in the contralateral field using the sensory probe task. Figure 7 illustrates the responses of a typical SC neuron to an acoustic sensory probe with the fixation point at (0°, 0°). The cartoon at the center of Figure 7 shows the position of the speakers relative to the fixation point. From top to bottom, panel A of Figure 7 illustrates vertical and horizontal eye position plotted as a function of time, a dot raster illustrating the responses of the neuron in individual trials, and a histogram normalized by the number of trials, summarizing the responses of the neuron in the trials shown. The data are plotted synchronized to the onset of the acoustic stimulus at 0 msec. The eye position traces corresponding to the other targets were similar to those plotted in Figure 7A, thus were omitted for simplicity. This neuron, recorded from the right SC, responded most strongly to stimuli presented from the left hemifield (Fig. 7B). The response of this neuron to a long duration (1000 msec) broadband noise stimulus consisted of a burst of 2-5 action potentials with a mean first spike latency of 18.3 msec.

Modulation of SC auditory responses by eye position

If the auditory responses of SC neurons are modulated by eye position, it would indicate that auditory RFs are dynamic and that they might not encode the position of sound sources in head centered coordinates. To address this issue we used the sensory probe task (Fig. 1B) with different fixation positions and a single source of acoustic stimulation. Figure 8 shows responses of a neuron that was modulated by eye position. The three columns show responses of a neuron in the right SC to the same speaker at (-18°, 0°), the area of space where the strongest responses could be evoked, while the cat was fixating three different positions: (±9°, 0°) and (0°, 0°). The largest responses (Fig. 8C) were recorded when the cat fixated an LED at (9°, 0°), the farthest away from the sound source, and the smallest responses (Fig. 8A) were recorded when the cat fixated the LED closest (-9°, 0°) to the sound source. Most of the neurons that were modulated
by eye position showed this type of modulation, though we also found neurons whose largest response occurred when the cat fixated the LED nearest the target. Trials from each of the three fixation conditions were presented in random order, thus long-term changes in variability should be averaged out. The results are summarized in Figure 8D, where mean spike count, normalized by the number of trials, is plotted as a function of horizontal fixation position. The error bars, representing 95% confidence intervals, indicate that the mean responses recorded at the three fixation positions were significantly different. We studied 106 neurons in the SC using the test shown in Figure 8 with a single speaker and 3-5 fixation positions, and three-fourths of them (81/106) were significantly modulated by eye position.

Do receptive fields shift?

Figure 8 illustrates the responses of a neuron to acoustic stimuli presented from a single source recorded at three different eye positions. Ideally one would like to extend these observations to a larger portion of a neuron’s RF to determine if such changes in neural response were due to a shift in the RF as a function of eye position. Recordings of this type were possible in 28 neurons, three of which are shown in Figure 9.

The motor error hypothesis predicts that auditory RFs will shift by an amount equal to the difference between the present eye position and the target, the motor error. Thus, if a neuron encodes the location of sound sources in motor error coordinates plotting the RFs for different points of fixation as a function of motor error should make the RF profiles superimpose. However, our RF profiles are undoubtedly incomplete because we did not sample in the caudal half of the auditory field, beyond 90º eccentricity, nor in the vertical dimension. For example, the responses shown in Figure 9A (left) are likely incomplete, because we only probed one flank of the RF. Nevertheless, the RFs of this neuron are better aligned when plotted as a function of motor error (Fig. 9A, right).

On the other hand the RFs shown in Figure 9B and Figure 9C are more complete because we captured the peak and both flanks. Neuron C6-59 (Fig. 9B) had a narrow horizontal RF, which, unlike most neurons, extended into ipsilateral space. The three functions, corresponding to the receptive fields measured in each of the three fixation conditions, are clearly separated at both the medial and lateral aspects of the field. Plotting the same data as a function of horizontal motor error aligns the three curves at both the medial and lateral edges, yielding a consistent measure of receptive field regardless of fixation position. Receptive fields with similar profiles, although broader, were obtained from other neurons (e.g., Fig. 9C). The receptive fields of this neuron’s medial edge were well aligned with the midline, as it is the case in most SC auditory neurons. However, unlike the neuron in Figure 9B, plotting the same data as a function of horizontal motor error increased the separation between the curves.

To determine the extent to which RFs shifted as a function of fixation position we computed a motor error index (MEI) as described in the Methods. The results of this analysis, taking into account all RF data available from each of the 28 neurons are shown in Figure 10A. For each neuron, the MEI due to leftward fixation is plotted against the MEI due to rightward fixation. Thus, RF shifts consistent with the motor error hypothesis will fall in the upper right quadrant, with perfect motor error expected at an MEI of (1, 1). No shift would be indicated by an MEI of (0, 0). The mean MEI from all 28 neurons (0.65, 0.66), although smaller than (1, 1), is significantly different from (0, 0) because the 95% confidence intervals do not encompass (0, 0). Thus, the horizontal RFs of the neurons in our sample shifted in a direction consistent with the motor error hypothesis.
To compare our results with those of Jay and Sparks (1987), who measured the magnitude of auditory RF shift in the monkey by taking into account only the medial edge, we computed the MEI for only the medial edge of the RF of our neurons as described in the Methods. The filled symbols in Figure 10B show the MEI for the medial edge of neurons that had a peak type of RF (n = 16), as defined in the methods, and the open symbols show the MEI for the remaining neurons (n = 13). The mean MEI from this analysis (0.81, 0.48) is also consistent with the motor error hypothesis, in agreement with Jay and Sparks (1987).

Potential contributions of the mobile pinnae

The modulation of auditory responses observed in the behaving cat appears to be similar to the modulation observed in the macaque monkey by Jay and Sparks (1987). Casual observation of the movements of the pinnae of both species indicates that cat’s pinna movements are more prominent, and thus more likely to change the acoustic input to the eardrum (Young et al. 1996), which can result in modulation of neuronal responses (Middlebrooks and Knudsen, 1987).

Previously, we have documented that orienting behavior of cats with restrained heads to acoustic and visual targets involves stereotyped and coordinated movements of both the eyes and the pinnae (Populin and Yin, 1998c). Because we required the cats to fixate on LEDs at different spatial locations to control eye position at the time of presentation of the acoustic stimuli, this would have systematically changed the position of the pinnae, which could have in turn altered the acoustic signals reaching the cat’s eardrums. Such changes in acoustic input could account for the modulation of auditory responses in the SC documented above.

Figures 11 and 12 illustrate the responses of two neurons, one which showed modulation by eye position and one which did not. The neuron in Figure 11 displayed atypical responses for it was best driven by acoustic stimuli presented from an ipsilateral source (-18º, 0º). We selected this neuron for illustration because the position of the left pinna was also recorded in the same trials. Five fixation positions were used (±18º, 0º), (±9º, 0º), and (0º, 0º). From top to bottom in Figure 11A, each row of panels illustrates horizontal eye position, left horizontal pinna position, the responses of the neuron in individual trials in raster format, and a histogram normalized by the number of trials summarizing the neuron responses. As expected from our previous observations (Populin and Yin, 1998c), the position of the left pinna at the time of stimulus presentation was a function of fixation position; a vertical arrow in each panel points to this portion of the pinna position records. The responses of neuron C6-75 to broadband noise stimuli presented from the same source at (-18º, 0º) were significantly modulated by fixation position and, possibly, pinna position (Fig. 11B).

Figure 12 shows that the movements of the pinnae are not necessarily related to modulation of acoustic responses by eye position. The auditory responses of this unit were not modulated by fixation position, although the position of the left pinna at the time of presentation of the acoustic stimuli also varied as a function of fixation position. This neuron was recorded in the right SC and the acoustic stimulus was presented from a target located at (-63º, 0º).

The ear movement traces in Figures 11 and 12 confirm that there were systematic changes in ear position related to the fixation of the LED at different spatial locations. Therefore there were also undoubtedly systematic movements of the pinnae during the collection of the data depicted in Figures 8-9, each of which showed modulation with eye position. Thus, the question arises as to whether the modulation with eye position was due to the change in acoustic input resulting from the movements of the pinnae or to an eye position signal that modulated the responsiveness
of the neurons. On the other hand the lack of modulation in Figure 12 demonstrates that changes in pinna position do not necessarily change the responsiveness.

**The effects of pinna immobilization**

The data presented in the previous section suggest the possibility that pinna movement associated with changes in fixation could account for the modulation observed in auditory responses of SC neurons. Changes in pinna position in the anesthetized cat have been shown to affect the spatial tuning of single SC neurons (Middlebrooks and Knudsen, 1987). To see if eye position, independent of ear position, is a source of modulation of auditory responses in the SC of the behaving cat, we immobilized the pinnae of one cat by cutting the auriculoposterior and temporozygomatic branches of the facial nerve bilaterally and recorded the responses of single SC neurons to broadband acoustic stimuli.

Typical eye and pinna movement data recorded simultaneously with the auditory sensory probe task from the intact cat are shown in Figures 11-12 before the immobilization surgery. At the time of these recordings, just before the pinnae immobilization procedure, subject’s C6 right pinna coil was broken so baseline data only from the left pinna were acquired at the time. We chose not to submit subject C6 to an additional surgical procedure to repair the broken coil because baseline data from this structure, demonstrating its movement, had already been recorded (Fig. 7 in Populin and Yin, 1998c). The pinna adopted different positions during the period preceding the onset of the acoustic probe, corresponding to the different positions of the fixation LEDs. The largest pinna movement was recorded when the cat fixated the LED ipsilateral to the pinna, at (-18°, 0º) and the smallest change when the cat fixated on the contralateral LEDs at (18°, 0º) (Fig. 11,12A). Also consistent with our previous findings (Populin and Yin, 1998c), are the short latency movement of subject C6’s left pinna after the onset of the acoustic target.

Figure 13 demonstrates that cutting the branches of the facial nerve was effective. After the pinnae immobilization procedure C6’s eyes continued to move normally (Fig. 13D), but there were no movements of either pinna when the cat fixated to the left or to the right (Fig. 13C, E). Both the left and right pinnae remained motionless for approximately 3 weeks, after which time they began to recover their ability to move, presumably due to nerve regeneration. The single neuron recordings presented below were carried out while subject C6’s pinnae were immobilized.

**Physiological recordings after pinna immobilization**

With the pinnae and head immobilized and the same acoustic stimuli presented while the cat fixated LEDs at different positions, any modulation of auditory responses in single SC neurons could not be attributed to changes in the acoustic input to the eardrum. Figure 14 illustrates the responses of a single neuron recorded from the left SC under those conditions. Broadband noise stimuli were presented from a speaker located at (63°, 0º) at about 10-15 dB above threshold. The responses were transient with little or no activity following the initial burst. Most importantly, they were significantly modulated by eye position (Fig. 14B). Most of the modulation was achieved within the initial burst. This neuron, like many in the deep and intermediate layers of the SC (Meredith and Stein, 1983; Populin and Yin, 2002) was bimodal and also responded to the visual presentation of the fixation LEDs when they were on the midline (Fig. 14A, center panel) and in the contralateral hemifield (Fig. 14A, right panels). Arrowheads point to this transient activity in the histograms (Fig. 14A) which is synchronized to
the presentation of the fixation LEDs, but because of the variable reaction time to make the saccade to the LED, they are not synchronized to the onset of the acoustic stimulus which was used to make the plots in Fig. 14.

We recorded from 24 neurons in a cat with immobilized pinnae, 20 of which were tested with only a single speaker. Approximately three weeks after the immobilization procedure some mobility returned to the pinnae; at this point the experiment was terminated and the brain tissue recovered for histological examination. The auditory responses of all 20 neurons were modulated in the cat with immobilized pinnae.

We were able to characterize the horizontal component of the RFs of four neurons more extensively. Two examples of those recordings are shown in Figure 15. In both cases the RFs became more misaligned when plotted as a function of motor error. Figure 16A shows the MEIs based on all available RF data from these neurons, and Figure 16B shows the MEIs computed only from the medial edge of the RFs. Data from one of the neurons were obtained at (±9º, 0º) and at (±18º,0º); which are plotted separately. Regardless of the type of analysis, none of the MEIs measured fell within the upper right quadrant, indicating that the neurons were modulated in a manner inconsistent with the motor error hypothesis. The mean and 95% confidence intervals from the intact cat data (Fig. 10) are shown for comparison.
DISCUSSION

There are four major results from this study: 1) saccades made by cats to acoustic targets with their heads fixed are not generally affected by the initial position of the eyes; 2) most of the neurons in the deep and intermediate layers of the SC that are responsive to acoustic stimuli are modulated by eye position, 3) those neurons from which more complete data from the horizontal component of the RF are available show that the modulation is consistent with the predictions of the motor error hypothesis and accounts for approximately 2/3 of the necessary compensation; and 4) the modulation with eye position is not due to the change in pinna position with visual fixation since it is still present when the ears are immobilized. We will discuss each of these results in turn below.

Behavioral results

The behavioral data show that sound localization accuracy is generally not affected by the deviation of the eyes in the orbit at the time of acoustic stimulus presentation. This is not a surprising finding, for grossly mislocalizing sounds simply because the eyes were not at the primary position would constitute a severe handicap for an animal. This means that the saccadic command to move the eyes must compensate for current eye position when a saccade is made to the same target from two different initial positions. For 3 of the 6 cats, there was no significant effect of initial eye position on the accuracy of saccades to targets and for 2 of the other cats there was a small but inconsistent effect. In only one cat (Fig. 5F, 6F) was there a consistent but small bias such that saccades starting from the left towards a vertical, but not a horizontal, target had a consistent error to the left while those starting from the right had a rightward error.

These results contradict Harris et al. (1980) in that they demonstrate that cats do compensate for deviations of the eyes from the primary position, but are in accord with both Hartline et al. (1995), who reported little effect of eye position on sound localization for deviations of about ±15°, and with Peck et al. (1995), who reported partial compensation only. These data are also consistent with those from human (Yao and Peck, 1997; Zahn et al. 1979) and monkey (Whittington et al. 1981) studies that found no effect of initial eye position on the accuracy of eye movements to acoustic targets.

Modulation of auditory responses in the deep and intermediate SC by eye position

The physiological data from the intact cat show that the responses of most SC auditory neurons (81/106) are modulated by eye position. In 28 neurons we were able to sample the RFs more extensively along the horizontal axis using different points of fixation (Fig. 9). These data allowed us to examine the extent to which the horizontal component of the RFs of auditory neurons shifted as a function of fixation position. Based on the MEIs computed from the RFs, 68% of the neurons were modulated by fixation position in a direction consistent with the motor error hypothesis. The percentage increased to 76% when the MEI was based on the medial edge.

Since many neurons in the deep and intermediate layers of the SC are multimodal, responding to both visual and auditory stimuli (Meredith and Stein, 1983), we should consider whether there is a visuomotor interaction that affects the eye position sensitivity demonstrated in these experiments. Sixty-three percent of the neurons we studied were indeed bimodal (see example in Fig. 14 and Populin and Yin, 2002). The example in Fig. 14 is typical of the short, transient visual response which is over for almost 400 msec by the time the acoustic stimulus is turned on. While it is possible that there is some lingering inhibitory effect of the visual response on the auditory response many hundreds of msecs later, the parsimonious explanation
would suggest that the effect is due to eye position and not to visuo-motor interaction. Note that at the time the acoustic target is turned on, the eye is always fixating the LED, so there should be an approximately constant visual input on every trial.

Thus, our data demonstrate that (1) the responses of 76% (81/106) of auditory neurons are modulated by eye position, (2) the modulation of 68% (19/28) of neurons from which a more complete sampling of the RF is available is consistent with the motor error hypothesis, and (3) the mean MEIs, (0.65, 0.66) computed from all available RF data and (0.81, 0.48) for the MEIs computed from the medial edge of the horizontal RFs, account for a compensation of approximately 2/3 of the shift required for perfect motor error.

Because the cats undershot the targets significantly (Fig. 5-6), a more appropriate measure of the motor error would be the distance between the initial position of the eyes and the apparent location of the targets as indicated by the end point of the saccade. We refer to this as behavioral motor error (BME). Ideally, we would have preferred to compute the MEI for each neuron using BME, not the physical location of the targets relative to the head. Such MEIs would have accounted for a larger proportion of the deviation of the eyes from the primary position. Although we could estimate the BME from our psychophysical results (Fig. 5-6), we were unable to compute BME for the neurons we studied for the following two reasons. The oculomotor range (approximately +/- 20 deg) of the cat limits this analysis to neurons with receptive fields in a very small portion of the auditory field of most SC neurons, which extend out to 90º or more. Releasing the head to allow the cat to orient to targets anywhere in the frontal hemifield would have prevented us from systematically manipulating the position of the eyes in the head at the time of stimulus presentation of the acoustic stimuli. Despite these limitations, our results, computed as a function of target position, agree with those of Jay and Sparks (1987), who reported a compensation of 54% in the SC of the monkey, and thus suggest that audio-visual interactions in monkey, a species with a larger oculomotor range, and cat SC are governed by similar rules. However, if we take into account the magnitude of the horizontal error made by our cats in localizing acoustic targets on the horizontal plane (Figs. 5-6), which on average was an underestimate of the targets by approximately 35%, the mean MEIs computed from all available RF data (0.65, 0.66) actually accounts for the observed behavioral responses.

Our results suggest that the modulation with eye position seen in SC neurons correlates better with the actual motor response of the cat (undershoot of about 35%) than to the motor error. In the monkey though there are data to suggest that the SC neurons are correlated better to motor error than to actual motor response (Stanford and Sparks, 1994; Frens and Van Opstal, 1998).

Effects of pinna immobilization on auditory responses in the deep and intermediate SC

Cats, however, move their pinnae in coordination with the eyes during the oculomotor tasks used in this study (Populin and Yin, 1998c). Macaque monkeys make large pinna movements in response to unexpected sounds, but do not seem to hold the position for an extended time (Jay and Sparks, 1987). The systematic changes in pinna position associated with fixating LEDs at different horizontal positions observed in our cats (Figs. 11, 12) led us to consider that the modulation of responses to acoustic stimuli of SC neurons could be, at least in part, due to changes in the acoustic input to the eardrum.

To determine directly if the modulation of auditory responses in single SC neurons was due to the changes in the acoustics, we surgically immobilized the pinnae of one cat. Failure to observe modulation would have supported the hypothesis that acoustic factors were solely responsible for the modulation seen in the intact cat. Because all 24 neurons studied in the
immobilized pinnae condition showed modulation by eye position, we reject the hypothesis that the modulation is caused exclusively by acoustic factors.

The patterns of the modulation of the spatial RFs documented in four neurons after immobilizing the pinnae, however, were inconsistent with our observations in the intact cat as assessed by the MEI (Figs. 15, 16). It is possible that this discrepancy is due to the method by which we computed the MEI. As pointed out above, a MEI computed using the perceived target location rather than the actual location is likely a more appropriate measure of the motor error. Several factors precluded us from computing such a metric. First, as was the case in the experiments with intact cats, it was not possible to document this cat’s localization accuracy at the range of eccentricities required to match those used to measure the auditory neurons’ RFs. Second, due to the limited recording time under pinnae-immobilized conditions afforded by the regenerating facial nerves (~ 3 wks), we were not able to conduct extensive psychophysical sound localization studies, focusing instead on the physiological recordings.

The data suggest that both an eye position signal and a pinna position signal contribute to shape motor error (Figs. 9, 10). In the intact cat copies of motor commands sent to the pinna may be used directly as a position signal or may be first evaluated against proprioceptive signals from the pinna. In either case, when the pinnae were immobilized, a mismatch would be expected between the desired position of the pinnae, the expected sensory consequences (i.e., acoustic filtering), and off course the eye position signal. While we are confident to have ruled out acoustical factors as the only source of the modulation, the small number of neurons recorded in the pinnae immobilized cat temper any conclusions drawn from the results following pinna paralysis.

Previous studies in the cat aimed at determining whether auditory RFs in SC neurons shift as a function of eye position produced conflicting reports. Harris et al. (1980) found no modulation in a sample of three neurons in the awake, untrained cat. They concluded that complex interactions between the visual and auditory representations in the SC are not needed because cats keep their eyes near the primary position most of the time, thus maintaining the alignment between the various sensory representations in the SC. Our results do not agree with this conclusion. Aside from their small sample of neurons, other methodological problems compromise their conclusions including cats that were untrained, stimuli delivered without acoustic shielding, and eye positions that were averaged over large ranges.

The conclusions of more recent studies (Hartline et al., 1995 and Peck et al., 1995) are consistent with our findings. However, Hartline et al. (1995) used essentially untrained cats with pinna coils that were taped to the ear and thus subject to slippage, only a small amount of data were presented making it difficult to evaluate their reliability, and they did not appear to have controlled for motor or other contributions that might result from eye movements. They collapsed responses over large ranges of eye and pinna positions, yet our data demonstrate that systematic changes in discharge rate take place with fixation positions that differed by as little as 9 deg. Peck et al. (1995) reported that their cats did not move their pinnae while performing their experimental tasks, though no records of pinna movements were presented. Our results (Figs. 11, 12, and Populin and Yin, 1998c) show that cats with immobilized heads move their ears extensively and systematically in response to both visual and acoustic stimuli, even after 1000s of trials. In agreement with our findings, Hartline et al. (1995) also reported that eyes and pinna tend to move in the same direction in a correlated fashion.

In summary, these results demonstrate the presence of an eye position signal that modulates the responses of SC neurons to acoustic stimuli. Eye positions signals in the SC are thought to
originate from corollary discharges (Guthrie et al., 1983) and not from proprioception (Nelson et al., 1989). Several issues remain unexplained by our data and will require further experimental work. First, the nature of the modulation in the cat with immobilized pinnae is dissimilar to that in the intact cat. We suggest that pinna position or the motor command to move the pinnae interact with eye position to modulate the SC cells but further work is needed. Second, the responses of some SC neurons to acoustic stimuli were not modulated by eye position. While static RFs are inconsistent with the predictions of the motor error hypothesis, they can provide a head-centered reference against which signals from neurons with dynamic RFs can be compared. Third, the RFs of some neurons become more misaligned when plotted as a function of motor error. Such responses, which would appear to contradict the concept of motor error, might still fit the hypothesis if they were inhibitory to neurons that provide a gain modulation that varies with eye position. Fourth, as Jay and Sparks (1987) found in the SC of the monkey, the magnitude of the shift in RF observed in most neurons did not compensate for the deviation of the eyes from the primary position at the time of presentation of the acoustic stimuli. but our data show that this undercompensation fits the undershooting saccades seen behaviorally. Behavioral motor error may be the important parameter in the SC.
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Figure 1.
Schematic representation of the behavioral tasks. (A) Standard-saccade task and (B) Sensory probe task. In both panels, from top to bottom: fixation LED, probe SPEAKER, hypothetical eye movement, and time line illustrating the events of a successful trial. All of the figures are plotted with events synchronized to the onset of the SPEAKER. For any given trial type [e.g. standard saccades from (0º,0º) to (18º,0º)] the required LED fixation time from “In LED window” to “LED OFF, SPEAKER ON” and the required speaker fixation time from “In SPEAKER window” to “SPEAKER off” were kept constant, though these varied from one trial type to another so that the cat could not predict how long these delays were.
Figure 2.
Schematic representation of the calculation of the motor error index (MEI) to quantify the mean shift in the RF as a result of fixation at two different positions. Shown are two hypothetical receptive fields plotted when the cat was fixating at the center (circles) and 15 degrees to the left (triangles). For each data point on both curves we measured the difference in azimuth between the two curves at the corresponding discharge rate keeping track of the shapes of the RF and the sign of the shift and interpolating linearly between data points when necessary. For example, the horizontal separation between the data point at 10° on the Left Fixation RF to the Center Fixation RF is -7.5°; while the separation between the data point at 20° on the Center RF to the Left Fixation RF was -7°. This shift was measured for all data points on both RFs where possible and averaged. For example, the shift for the left-most point on the center RF and the rightmost point on the left fixation RF cannot be measured. The mean RF shift of this unit, computed by taking into account all data points, was -7.6, which yields an MEI of 0.51 for a fixation point located 15° to the left.
Figure 3.
Photograph of Cat6’s midbrain illustrating the method used to determine electrode penetration placement. Metal pins were inserted caudal to the left SC and rostral to the right SC. The position of the electrode penetrations, illustrated by the cross pattern, was plotted relative to the position of the pins. SC: Superior colliculus; IC: inferior colliculus.
Figure 4.
Most eye movements to acoustic targets consisted of a single saccade. Vertical (A) and horizontal (B) components of eye movements to an acoustic target at (0º, 24º) from three different starting positions (±4º,0º), and (0º,0º) are plotted synchronized to the onset of the acoustic target at time 0 msec.
Figure 5.
Effect of initial eye position on sound localization accuracy. Eye movements to acoustic targets initiated from different fixation positions along the horizontal plane (0° elevation). Each trace represents a single trial plotted from the time of acoustic stimulus presentation to the time in which the cat was rewarded for correct performance. The dots that make up each trace represent digital samples of the analog signals obtained from the eye coil system (at 500 Hz). The asterisks represent the acoustic targets and arrows in each plot indicate the direction of the eye movements.
Figure 6.
Summary of sound localization performance from six cats. The position of the acoustic targets is represented by asterisks, initial eye position is represented by filled symbols located along the main axes, and mean final eye position is plotted with open symbols matching the corresponding initial eye positions. The horizontal and vertical errors bars represent 95% confidence intervals.
Figure 7.
Typical auditory neuron in the right SC is excited most strongly by a source located in contralateral field. The cat was required to fixate an LED at the primary position, depicted by a “+” sign. Auditory stimuli were presented from the four speaker positions illustrated in the cartoon at the center of the figure: (±18°, 0°), (0°, 18°), and (0°, -23°). The top panels illustrate vertical and horizontal eye position, dot raster shows the responses of the neuron in individual trials (the tickmarks represent action potentials), and a histogram normalized by the number of trials summarizing all trials plotted. The ordinate of the histograms represents the number of spikes per bin (10 msec), normalized by the number of trials. Eye position traces have been omitted from the other three plots for simplicity.
Figure 8.
Modulation of single auditory SC neuron responses by fixation position. The cartoons at the top of the figure illustrate the experimental arrangement and the expected movements of the pinnae. The auditory sensory probe task was used. The acoustic stimuli were presented from a speaker located at (-18°, 0°) while the cat fixated LEDs at (-9°,0°) (A), (0°,0°) (B), and (9°,0°) (C). (D) Summary of the responses representing the mean number of spikes per trial. The error bars represent 95% confidence intervals.
Figure 9.
Examples of receptive fields from single neurons recorded from the intact cat at three different fixation positions plotted as a function of horizontal speaker positions (left column) and as a function of motor error (right column).
Figure 10.
Summary of Motor Error Index (MEI) from the intact cat. (A) Leftward MEI plotted as function of rightward MEI computed by taking into account the horizontal receptive field of all 28 neurons studied with multiple speaker positions in 5 cats. MEIs from two neurons were computed at more than three fixation positions, resulting in 29 data points. (B) Similar plot of MEIs computed by taking into account just the medial edge of the neurons’ receptive fields (square symbols); round symbols replot those MEIs from A from neurons that did not have peaked RFs. The standard bars represent 95% confidence intervals for the mean MEIs. See Results.
Figure 11.
Single neuron responses modulated by fixation positions. (A) The top panels illustrate horizontal eye position; five fixation positions ($\pm 18^\circ$, $0^\circ$), ($\pm 9^\circ$, $0^\circ$), and ($0^\circ$, $0^\circ$) were used. The position of the left pinna plotted as a function of time is plotted below the eye position. The vertical arrows point to the different horizontal positions adopted by the cat’s left pinna during the fixation period before the onset of the acoustic probe. (B) Summary of the neuron’s responses normalized by the number of trials in each condition.
Figure 12.
Un-modulated single neuron activity and left pinna movement data recorded in the same trials. The organization of this figure is the same as in Figure 12.
Figure 13.
Pinnae immobilization experiment. (A-B) left pinna and eye baseline behavior recorded from the intact cat in the context of the sensory probe task. The fixation targets were located at (±18º, 0º) and the acoustic stimuli at (-18º, 0º). The fixation LED was turned on at about -1000 msec for the right fixation trials and at about -750 msec for the leftward trials (the delay between the time that the cat acquired the fixation LED and the acoustic stimulus was turned on were different for these two classes of trials). The acoustic stimuli were turned on at time 0. (C, E) left and right pinna and (D) eye behavior recorded from the cat with immobilized pinnae in the context of the sensory probe task. For both leftward and rightward cases the fixation LED was turned on at about -750 msec. The same 1000 msec broadband (0.1-25 kHz) noise acoustic stimuli were used in all conditions. After the immobilization procedure the pinnae of the cat neither moved in association with the eye movements or in response to the sound; the pinna position traces in C and E were centered at 0 deg.
Figure 14.
Single neuron responses to acoustic stimuli recorded in the cat with immobilized pinnae. The acoustic stimulus was presented from a speaker at (63°, 0°). The responses of this neuron were larger for fixation positions closer to the target speaker. This neuron was recorded in the left SC.
Figure 15.
Examples of receptive fields from single neurons recorded from the pinnae immobilized cat at three different fixation positions plotted as a function of horizontal speaker positions (left column) and as a function of motor error (right column).
Figure 16.
Summary of Motor Error Index (MEI) from the pinnae immobilized cat. (A) Leftward MEI plotted as function of rightward MEI computed by taking into account the entire receptive field of all 28 neurons studied with multiple speaker positions. The mean and 95% confidence intervals of the population from intact cats from Figure 10 are indicated by the bars. (B) Similar plot of MEIs computed by taking into account the medial edge of the neurons’ receptive fields.