Sound-Localization Performance in the Cat: The Effect of Restraining the Head

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Submitted 21 July 2004; accepted in final form 10 October 2004


In oculomotor research, there are two common methods by which the apparent location of visual and/or auditory targets are measured, saccadic eye movements with the head restrained and gaze shifts (combined saccades and head movements) with the head unrestrained. Because cats have a small oculomotor range (approximately ±25°), head movements are necessary when orienting to targets at the extremes of or outside this range. Here we tested the hypothesis that the accuracy of localizing auditory and visual targets using more ethologically natural head-unrestrained gaze shifts would be superior to head-restrained eye saccades. The effect of stimulus duration on localization accuracy was also investigated. Three cats were trained using operant conditioning with their heads initially restrained to indicate the location of auditory and visual targets via eye position. Long-duration visual targets were localized accurately with little error, but the locations of short-duration visual and both long- and short-duration auditory targets were markedly underestimated. With the head unrestrained, localization accuracy improved substantially for all stimuli and all durations. While the improvement for long-duration stimuli with the head unrestrained might be expected given that dynamic sensory cues were available during the gaze shifts and the lack of a memory component, surprisingly, the improvement was greatest for the auditory and visual stimuli with the shortest durations, where the stimuli were extinguished prior to the onset of the eye or head movement. The underestimation of auditory targets with the head restrained is explained in terms of the unnatural sensorimotor conditions that likely result during head restraint.

I N T R O D U C T I O N

The primary goal of psychophysical studies of sound localization is to obtain the best possible estimates of the perceptual performance of the observer. These estimates, typically quantified in terms of localization accuracy and precision (or consistency), will depend not only on the observer’s perception of location but also on the method by which perceived location is reported. Consequently, any experimental measurement of localization accuracy and precision reflects a combination of a sensory component and a component associated with the behavioral response method. In general, experimental methods have sought to minimize the latter component. Various response methods that have been commonly used in human studies, such as verbally reporting the spherical coordinates of apparent location (Stevens and Newman 1936; Wightman and Kistler 1989) or indicating location on a spherical model of the testing apparatus (Gilkey et al. 1995), are not readily adapted to studies in animals.

From an ecological standpoint, the most natural response method is to point or orient to the location of the source with the head (Knudsen et al. 1979; Makous and Middlebrooks 1990; May and Huang 1996; Perrott et al. 1987) or with eye or gaze position (Frens and Van Opstal 1995). It is a natural tendency for animals to make an orienting response consisting of coordinated movements of the head, eyes, and body toward a sound’s source. Coordinated movements of the eyes and head are called gaze shifts (or gaze saccades), whereas eye saccades refer to movements of the eyes in their orbits. In the context of sound localization, it has been hypothesized that one of the primary functions of the auditory system is to determine the location of sounds so that the eyes, which have much higher spatial acuity, can be directed toward the source for further inspection (Heffner and Heffner 1992). Therefore eye, gaze, or head position represents a practical pointing method for measuring sound-localization abilities in animals such as cats, a common animal model for the study of the anatomy, physiology, and psychophysics of sound localization (Yin 2002).

Here we assess two common methods of measuring the accuracy and precision of sound localization in the cat, head-restrained eye saccades and head-unrestrained gaze saccades. Both methods have advantages and disadvantages. When the head is restrained, it is in a known location, useful for estimating the acoustical cues to location, and it is more stable, which is useful for chronic physiological recordings and for delivering the food reward. But the behavioral responses are limited to the oculomotor range of the cat (approximately ±25°), which leaves a considerable range of unexplored auditory space. With the head unrestrained, although the behavior is more natural and unrestricted and the response range can be greater, there can be more uncertainty about the actual acoustical cues to location from trial to trial. Here we show that gaze saccades to visual and auditory targets are more accurate than eye saccades with the head restrained, particularly for short-duration stimuli. Portions of this data have been presented (Populin et al. 2000).

M E T H O D S

Subjects and surgery

All surgical and experimental procedures complied with the guidelines of the University of Wisconsin Animal Care and Use Committee and the National Institutes of Health. In three adult female domestic cats, we implanted a stainless steel head post and fine wire coils

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Experimental apparatus and stimuli

All experiments were conducted in a dimly illuminated (or dark) sound-attenuating chamber (2.2 × 2.5 × 2.5 m, IAC, Bronx, NY). All walls and major pieces of equipment were covered with sound-absorbing acoustic foam (10.2 cm, Sonex, Ilbruck, Minneapolis, MN) to minimize acoustic reflections. The magnetic search coil (CNC Engineering, Seattle, WA) technique (Fuchs and Robinson 1966) was used to measure the positions of the eyes and the analogue output of the coil system was saved to disk by sampling at 500 Hz.

Targets in these experiments consisted of both visual and acoustic stimuli presented from one of 15 different locations distributed along two arcs (62-cm radius), one on the horizontal and one on the vertical meridian. Acoustic stimuli were delivered from one of 15 Radio Shack (Fort Worth, TX) super tweeters, model 40-1310B, (modified to transduce low frequencies) with similar frequency response characteristics. Visual stimuli consisted of a 2.0-mm-diam red (λ_max = 635 nm) LED located at the center of each speaker. The speakers themselves were hidden from view behind a black translucent cloth through which illuminated LEDs could be easily seen. The voltage waveforms for the acoustic stimuli were generated digitally by a custom-built digital stimulus system with built-in attenuators and played out at a rate of 100 kHz to a 15 channel multiplexer. The 15 available outputs of the multiplexer were connected to individual audio amplifiers that drove the 15 speakers (see Populin and Yin 1998a for details). The overall level of each acoustic stimulus used was varied from trial to trial by ±6 dB in 2-dB steps to minimize the possibility that differences in the frequency responses of the speakers could assist performance.

Acoustic stimuli consisted of a broadband noise (~1.5–25 kHz) of three different durations: 1,000, 164, and 15 ms (additional durations were examined in some cats in the head-unrestrained condition). The overall amplitudes of the three different duration stimuli were adjusted to maintain approximately the same power spectrum. The visual stimuli consisted of illuminations of the LED for two different durations, 1,000 and 25 ms. In the first experiment, the heads of the cats were restrained in the center of the coils comprising the magnetic search coil system (see Fig. 1 of Populin and Yin 1998a). In the second experiment, the heads were freed but a body restraint helped to maintain the position of the head within the center of the coil system. All aspects of the experiments including selection of the visual or acoustic stimuli, the location of the target speaker and/or light-emitting diode (LED), the acquisition of the eye position, etc. were under the control of a Microvax-2 computer (Digital Equipment, Maynard, MA).

Eye-coil calibration

In both the head-restrained and - unrestrained experiments, the eye coils were calibrated using a behavioral procedure where the cats were required to look at each of the LEDs, in turn (Populin and Yin 1998a). No training was required for this because the cats usually looked at the LEDs when suddenly illuminated in the darkened chamber. When the cat visually fixated one of the LEDs, the output of the coil system was sampled and its value stored on the computer. This was repeated two to three times for each of the LED locations. The vertical and horizontal components of these final eye positions were separately fit with first-order linear functions relating the output of the coil system to the target angle. The coefficients of the fit (slope and intercept) were then used by the data collection software to convert the voltage output of the coil system to degrees of visual angle. Within the spatial range of this experiment (±25°), the voltage output of the coil system and the location of the target were well fit by a linear function (coefficients of determination for fits exceeded 0.96).

Psychophysical procedure and training

The cats were on a controlled-access diet for 5–6 day/wk. Water was always available. During the psychophysical task, the cats earned food rewards, which consisted of a puree of canned cat food, finely ground cat chow, and water, that were delivered via a peristaltic pump after each “successful” trial. While the cats typically worked until they were satiated during each day of testing, their weights were monitored daily, and we ensured that it was maintained within 15% of the original weight.

Using operant conditioning, the cats were trained to make orienting eye saccades (head restrained) and gaze saccades (head unrestrained) to the location of LEDs. The cats were rewarded under computer control of a Microvax-2 computer (Digital Equipment, Maynard, MA). The cats were required to look at each of the LEDs, in turn (Populin and Yin 1998a). No training was required for this because the cats usually looked at the LEDs when suddenly illuminated in the darkened chamber. When the cat visually fixated one of the LEDs, the output of the coil system was sampled and its value stored on the computer. This was repeated two to three times for each of the LED locations. The vertical and horizontal components of these final eye positions were separately fit with first-order linear functions relating the output of the coil system to the target angle. The coefficients of the fit (slope and intercept) were then used by the data collection software to convert the voltage output of the coil system to degrees of visual angle. Within the spatial range of this experiment (±25°), the voltage output of the coil system and the location of the target were well fit by a linear function (coefficients of determination for fits exceeded 0.96).

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control if they maintained for a period of time (600–1,000 ms) their eye position after the eye/gaze saccade in the vicinity of the target as determined by a square-shaped electronic acceptance window that was centered on the target location. During training, the acceptance windows for the visual trials were gradually decreased to ±4–5°, but the windows for the auditory trials remained large (±8–12°). This was done for the auditory trials to encourage the cats to look to the apparent location of the sound source without training them to look to a particular location in space to get a reward (see Populin and Yin 1998a). However, all data were analyzed, even if the cat did not get the trial “correct.”

All data presented in this paper were collected in the saccade psychophysical task. Here, the cat was initially required to fixate an LED presented from 1 of the 15 locations and maintain fixation within the acceptance window for a variable period of time (600–1,000 ms). If the cat satisfied this initial fixation condition, then simultaneously the fixation LED was extinguished and an acoustic or visual target was presented from 1 of the 15 locations within the oculomotor range of the head-fixed cat (approximately ±25°). The cat was then required to make a saccadic eye movement (or gaze saccade in the unrestrained condition) to the apparent location of the target and maintain fixation at that location for 600–1,000 ms. If during this time the cat’s eye or gaze position was within the specified acceptance window, the cat was given a food reward. In the head-restrained condition, the food reward was delivered via a plastic tube that was held firmly in place near the cat’s mouth so it could easily be licked. In the head-unrestrained condition, we developed a small lightweight (40 g) aluminum head-set like apparatus, which could be attached to the head post, that held the feeding tube near the mouth. This feeding system, which moved with the head, allowed the cat to receive the rewards as in the fixed head condition. The cats quickly learned to perform the psychophysical tasks using this apparatus. All cats were initially trained with their heads restrained. The head was restrained by a horizontal bar (12 × 12 mm, 40 cm in length) that was designed to attach to the head post of the cat from behind the cat’s head (see Fig. 1, Populin and Yin 1998a). With this arrangement, the heads of the cats could be restrained while minimizing any disruption of vision, movements of the pinnae, or the acoustical cues to sound location.

Analysis of final eye and gaze position

The dependent variable in these experiments was the final two-dimensional eye or gaze position at the completion of the saccadic eye movement or saccadic gaze shift to the apparent location of the target. Examples of saccadic eye movements and gaze shifts are shown in Fig. 1, A and B, respectively. We used the method outlined in Populin and Yin (1998a) to compute separately the final horizontal and vertical eye or gaze position. An example of the analysis method is described in the preceding text, the horizontal and vertical components of the target locations with a single value. This then allows for easy comparison of subjects, and across different studies. Moreover, gain, defined simply as the ratio of the eye or gaze saccade amplitude and the target amplitude, is a commonly used and therefore a readily understood statistic other than gain would have led us to the same conclusions made here. To confirm this prediction, we also computed the errors in localization of each target by measuring the horizontal

eye/gaze shift were computed for each trial, separately for horizontal and vertical components. The motor error was defined as the difference between the target-in-space position and the initial eye/gaze position. In other words, the motor error describes the magnitude of the eye/gaze shift needed to acquire the target position given the initial eye/gaze position. Note that only when the eyes are initially directed at exactly (0°,0°) will the motor error be equivalent to the absolute position of the target in space. In our experiments, because the cats were always required to fixate the LED at 0°,0° before the eye/gaze saccade, the motor error is usually nearly equal to the position of the target in space. The eye/gaze shift was defined as the angular magnitude and direction of the eye or gaze saccade.

To obtain a quantitative measure of the localization performance across all target locations, a linear function was fit to the plots of eye/gaze shift versus motor error; separate functions were fit for the azimuthal and for the elevational components of the target locations. This procedure was performed for each experimental condition (head restrained and unrestrained) as well as for each stimulus type (visual and auditory) and duration. The coefficients of the fits are indicators of localization performance. For example, the slope of the response-target localization function, which we shall refer to as “gain,” indicates the accuracy with which the cats localized the targets. A gain of 1.0 indicates that, on average across all trials and all target positions, the cats located the targets to their actual positions, whereas gains <1.0 indicate that the target locations were underestimated. Standard statistical bootstrapping techniques (Efron and Tibshirani 1986) were used to obtain an estimate of the 95% confidence intervals of the gain. Here, for a given stimulus configuration (e.g., 15-ms duration noise, head-restrained), 1,000 synthetic data sets, containing exactly the same number of trials as the empirical data set, were created by randomly sampling, with replacement, localization data from individual trials from the empirical data sets for each cat separately. As described in the preceding text, the horizontal and vertical components of the behavioral responses were analyzed separately. A linear function was fit to each synthetic data set resulting in 1,000 measurements of the gain, from which the 95% confidence interval was obtained by first sorting the 1,000 gains and then finding the 25th and 97.5th values (corresponding to the 2.5 and 97.5 percentiles, respectively). Using the empirical data set, we also computed the SD of the residuals of the fitted function, again separately for the horizontal and vertical components of the responses, which represents the distribution of behavioral responses about the mean gain. This latter value gives a numerical estimate of the precision (or consistency) of the localization responses, which we refer to as δ.

The gain metric as a quantitative measure of localization accuracy allows for localization performance to be summarized for many target locations with a single value. This then allows for easy comparison of localization performance across different experimental conditions (e.g., head restrained/unrestrained, stimulus duration, etc), across subjects, and across different studies. Moreover, gain, defined simply as the ratio of the eye or gaze saccade amplitude and the target amplitude, is a commonly used and therefore a readily understood metric in studies of the oculomotor system. Yet there are also some important caveats. First, as we have used it, the gain metric assumes that the horizontal and vertical components of the two-dimensional errors in source localization are independent, which may or may not be the case. Second, it assumes that accuracy is linearly related to target eccentricity. Third, the gain metric is appropriate only for target locations and responses that span a restricted area of space. Gain is not appropriate when targets and responses occur at very high or very low elevations because for these positions a very small spatial error in localization amounts to a very large number of degrees in azimuth. Because the targets and responses in this study were generally restricted to ±25° in azimuth and elevation, we are confident that the use of a statistic other than gain would have led us to the same conclusions made here. To confirm this prediction, we also computed the errors in localization of each target by measuring the horizontal
and vertical angles separating the final gaze position and the absolute position of the target in space. We preserved the direction of the errors so that the average of these signed errors indicates whether and by how much each target was under- (errors < 0°) or overestimated (errors > 0°). To summarize localization accuracy for each cat and each experimental condition, the mean signed error in azimuth and in elevation for that condition was computed by taking the average of the signed errors separately for the four targets in azimuth and the four targets in elevation, respectively. The variability of the horizontal and the vertical components of the gaze shifts for each location were represented by the SD of the horizontal and the vertical components of the gaze shifts about the mean final gaze position, respectively. To summarize the variability, the mean SD in azimuth and elevation was computed by taking the average of the SDs separately for the four targets in azimuth and the four targets in elevation, respectively. Readers are referred to Leong and Carlile (1998) for a discussion of alternative methods for statistical analysis of localization data.

RESULTS

These experiments were designed to determine whether there are differences in the abilities of cats to localize sounds using gaze saccades with their heads unrestrained compared with using eye saccades with their heads restrained. The results and statistical analyses are based on the localization performance of three adult female cats (cats 17, 18, and 21). Experimental sessions were chosen for analysis based on the level of a cat’s motivation that day and the presence and number of the particular trial types of interest for this experiment. Data from all trials from the chosen sessions were used, even those that were not “successes” as determined by the reward criteria, and are included in the analysis. Because the cats performed similarly, we shall use data from different cats to highlight common aspects of their behavior as well as to illustrate the variability between animals. All data were taken from the saccade psychophysical task (Populin and Yin 1998a) in which the initial fixation LED was located at the central position (0°, 0°). Because the goal of this paper was to examine the localization performance of the cats and not necessarily the kinematics of their responses, we did not determine here whether the eye or gaze saccades were well described by their main sequence (i.e., Bahill et al. 1975) or measure the relative contributions and timing of eye- and head-movement components of the gaze saccades. Hence, our use of the term “saccade” refers only to the general nature of the behavioral responses of the cats.

Visual and auditory localization with the head restrained

Figure 1A shows typical horizontal saccadic eye movements as a function of time from one cat (cat 18) to long-duration (1,000 ms) visual and auditory stimuli from four target locations on the horizontal plane. These results agree qualitatively with our earlier reports (Populin and Yin 1998a). In general, based on visual inspection of saccade traces, eye movements to visual targets were more accurate and precise than those to auditory targets in the same spatial positions. In auditory trials, eye movements with the head restrained typically underestimated or “undershot” their targets.

Figure 2A shows the final horizontal and vertical eye position for the eight most extensively tested target locations from another cat (cat 21) in the head-restrained condition for long-duration visual (left) and auditory (right), and transient auditory (middle) stimuli. The saccades to visual targets were tightly grouped (good precision) and were located near each target in azimuth and elevation (good accuracy), whereas the saccades to auditory targets undershot (poorer accuracy) the target locations and were often more scattered (less precise).

To quantify these qualitative observations, the six figures constituting Fig. 2B show scatter plots of eye motor error (i.e., the angular distance between the initial position of the eyes and the actual target) versus actual eye displacement (i.e., the angular distance and direction that the eyes moved) for cat 21 for the same three stimulus conditions. Separate plots were made for horizontal and for vertical components of the responses. The correlation coefficients of the fitted functions for all conditions and all cats were significant (average r = 0.93 ± 0.05). As was apparent in the raw data shown in Figs. 1A and 2A, the responses of the cat exhibited more undershooting of the target location in both azimuth and elevation, resulting in lower gain values for both auditory and visual targets. The responses were also often less precise (greater δ) for auditory than visual targets. Moreover, both of these differences were even more pronounced for the transient auditory than for the long-duration auditory stimuli. Results for the head-restrained condition in terms of gain and δ for each of the three cats are summarized in Table 1 for the longest and shortest duration auditory and visual stimuli. For comparison, the mean signed horizontal and vertical errors and horizontal and vertical response SDs for each cat and each stimulus condition were computed (see Methods). Table 2 shows the mean signed errors and SDs averaged across the three cats for the longest- and shortest-duration auditory and visual stimuli. [Note that the mean gains and δ’s averaged across cats are highly and significantly correlated with the mean signed errors (r = 0.98, P < 0.001, n = 16) and SDs (r = 0.92, P < 0.001, n = 16) averaged across cats for the data from the conditions shown in Tables 1 and 2.]

Visual and auditory localization with the head unrestrained

Figure 1B shows horizontal gaze movements of cat 18 to long duration visual and auditory targets with the head unrestrained. Unlike the case with the head restrained (Fig. 1A), the undershooting of auditory targets was reduced. Similar gaze shifts were made to targets varying in elevation along the median plane (not shown). In the same format as Fig. 2A, Fig. 3A shows final gaze position for cat 21 with the head unrestrained. Even more so than in Fig. 2A, the responses to visual trials were well grouped and located near each target in azimuth and elevation. The responses to auditory trials were more accurate with less undershooting than in the head-restrained trials. The six figures constituting Fig. 3B show that although accuracy of localization improves compared with the head-restrained condition, indicated by gain values near 1.0, scatter about the mean remained constant or, in the case of short-duration stimuli, actually increased. In other words, for this and the other cats, although localization accuracy improved by freeing the head, the precision of the responses was similar to, or worse, than that found with the head restrained.

Results for each of the three cats are summarized in Table 1 in terms of gain and δ and in Table 2 in terms of mean signed error and mean SD for the longest- and shortest-duration
auditory and visual stimuli tested in both head-restrained and unrestrained conditions. For the unrestrained condition, gaze shifts to targets with long-duration auditory stimuli were as accurate as those to visual stimuli in both azimuth and elevation. This is evidenced by both gain values near 1.0 and signed error values near 0.0°. Moreover, localization accuracy to transient auditory stimuli was excellent and was similar to the accuracy to long-duration stimuli in azimuth and nearly as accurate in elevation.

Head-unrestrained gaze saccades are more accurate than head-restrained eye saccades

Plots like those shown for cat 21 in Figs. 2 and 3 were constructed for each of the three cats and performance was quantified, separately for the azimuthal and elevational components of the responses, in terms of response gain and scatter about the mean as described in METHODS. Figure 4 summarizes the localization performance for all three cats. The gains of the localization functions with the 95% confidence intervals of the gain are plotted separately for visual (left) and auditory (right) conditions as well as for the azimuthal (bottom) and elevational (top) components of the responses as a function of stimulus duration for both head-restrained and unrestrained conditions. Differences between the head-restrained and unrestrained conditions are summarized by the △, ○, and □ and △, ●, and ■, respectively. The most striking differences are evident in the auditory stimuli varying in azimuth (bottom right; see also Table 2 for signed errors). The overall pattern of the three cats’ behavior was similar across conditions although they produced somewhat different absolute accuracies (gains). For example, cat 21 was less accurate locating transient visual stimuli (25 ms) with the head restrained compared with the other two cats, whereas cat 18 was less accurate locating auditory stimuli with the head unrestrained than the other cats. One exception to the behavioral consistency between the cats was that in the head-unrestrained condition with targets varying in azimuth, cat 18 undershot (gain < 1.0) and cat 21 overshot (gain > 1.0) for short stimulus durations, and cat 17 located both transient and long-duration stimuli with roughly equal accuracy (gain = −1.0) without under- or over-shooting. This variability may be taken as an estimate of the individual differences in localization performance of cats. Table 1 summarizes the localization performance, in terms of gain and precision, for each cat for the shortest- and longest-duration auditory and visual stimuli with the head restrained or unrestrained.

As assessed by the gain of the localization functions (Fig. 4 and Table 1), localization with the head restrained was clearly more accurate for visual than auditory targets for all cats except for short-duration stimuli with one cat (cat 21). The signed errors in Table 2 support this finding. This was not the case in the head-unrestrained condition where localization for all cats...
was nearly as accurate to auditory as visual targets (with the exception of cat 18 with short-duration targets). On average, the cats looked to within 1° of targets positioned in azimuth and to within 2–3° for targets positioned in elevation (Table 2). Accuracy for localizing long-duration visual targets in elevation was comparable in head-restrained and -unrestrained conditions and only a slight improvement in accuracy in azimuth was accomplished by freeing the head (e.g., Fig. 1 and Tables 1 and 2). The results with long-duration visual stimuli demonstrate the important fact that with the head restrained, all the cats could saccape fairly accurately to each of the target locations tested in this study, indicating that any underestimation of target location in this condition was likely not due to mechanical limitations of the oculomotor system. In contrast, localization accuracy improves substantially by freeing the head for long-duration auditory targets varying in elevation and even greater for targets varying in azimuth. Altogether across cats, there were 34 total conditions for which we could evaluate the effect of head restraint on localization precision. In 10/34 conditions, precision improved (smaller $H_9254$) in the head-unrestrained condition. These improvements occurred only for long-duration visual and auditory targets or short-duration

### TABLE 1. Summary localization statistics of gain and $\delta$ for the three cats

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<th></th>
<th>Visual</th>
<th>Auditory</th>
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<tr>
<td></td>
<td>Short, 25 ms</td>
<td>Long, 1,000 ms</td>
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<tr>
<td></td>
<td>Fixed</td>
<td>Free</td>
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### $\delta$

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<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>3.14</td>
<td>2.80</td>
</tr>
<tr>
<td>Azimuth</td>
<td>2.50</td>
<td>3.41</td>
</tr>
</tbody>
</table>

Each entry for the signed error indicates the mean ± SD of the signed error averaged across the three cats. Negative errors indicate underestimation of target location while positive errors indicate overestimation. Each entry for the SDs indicates the mean ± SD of the response SD, averaged across the three cats. See METHODS for details on how errors were computed.
visual targets. Surprisingly, however, in the remainder of conditions, precision worsened (larger δ). However, in the majority of conditions (22/34), the effect of unrestraining the head on localization precision was generally small, with a <20% increase in δ relative to the head-restrained condition. These results are supported by the mean response SDs in Table 2.

Typically for all cats, for both auditory and visual targets, in both azimuth and elevation, and in head-restrained and -unrestrained conditions, localization accuracy improved (increasing gain and reduced signed error) with stimulus duration (Fig. 4 and Tables 1 and 2). The improvement was more dramatic, particularly for the head-restrained condition, for visual than auditory stimuli as seen in the steeper slopes in Fig. 4, left as compared with right. The improvements in localization accuracy in the head-unrestrained condition as auditory stimulus duration increased were confined mostly to targets varying in elevation as localization was quite accurate already for short-duration targets varying in azimuth (Table 1 and 2). In all, however, the most striking finding was the improvement in the localization of auditory targets with the head unrestrained compared with restrained at any stimulus duration (Fig. 4, bottom right, and to a lesser degree, top right).

**Control experiments**

Because the cats were initially trained and tested with their heads restrained, it is not an unreasonable hypothesis that the improvement in sound localization in the unrestrained condition might have resulted from the cats learning to utilize the acoustical cues to location using strategies that were not initially apparent to them in the initial restrained condition. If so, this strategy might then be used when the cats’ heads were again restrained to effect improved accuracy. To test that hypothesis, we reexamined the localization performance of two cats in the head-restrained condition after they had been exposed to and tested with their heads unrestrained. Relative to the initial restrained data, Fig. 5 reiterates (for cat 21) the finding that freeing the head results in improvements in sound-localization accuracy as indicated by the systematic increases in gain for all conditions tested, particularly in azimuth. Figure 5 also shows that sound-localization accuracy with the head restrained after the cats had exposure and training in the

![Fig. 3. Same as Fig. 2 except for head-unrestrained condition.](http://jn.physiology.org/DownloadedFrom/10.220.32.246)
unrestrained condition was comparable to the initial head-restrained localization. This indicates that our cats likely did not learn some new sound-localizing strategy with the head free that was transferable and could subsequently be used in head-restrained localization. Hence, the improvement in performance with the head unrestrained is likely the result of allowing the cat to move the head and eyes in a coordinated fashion rather than their adopting a different strategy.

As we had shown with eye saccades in our previous study of localization in head-restrained cats (Populin and Yin 1998a), we wanted to verify here that our cats also made gaze saccades to targets based on acoustic cues associated with the sound source location, and not to the locations of remembered visual targets. In one session, we shifted a subset of the loudspeakers positioned along the horizontal plane by 4.5° without presenting visual stimuli from the new locations. Trials involving these new test targets were randomly interspersed with trials to visual and auditory target locations at other positions; visual targets were not presented at the shifted target locations. The final eye position for the novel targets were shifted by approximately the same amount as the target. For example, for the most extensively-tested cat in this control condition (cat 18), with shifted auditory targets (1,000-ms duration) at (±13.5°,0°) and (±22.5°,0°), the resulting gain of the localization responses was 0.95 (n = 102). These results are nearly identical to those produced when the targets were in their standard positions (gain = 0.93; Table 1). This indicates that the cats perceived the changes in location of the acoustic targets and could direct their behavioral responses to these locations. Hence, our cats oriented to the apparent locations of the sound sources and not to remembered target locations.

**DISCUSSION**

It is a natural tendency of animals to orient toward the spatial locations of visual and acoustic objects. Orientations can consist of head, eye, pinna, and whole-body movements. In previous studies of sound localization in the cat from our lab (Populin and Yin 1998a; Tollin and Yin 2003a,b), we have taken advantage of this tendency to measure performance in head-restrained cats that were required to make saccadic eye
movements to the apparent location of the targets. In this paper, we tested the hypothesis that by allowing the cats to make more natural gaze saccades (joint eye and head movements) to auditory and visual targets, localization accuracy and precision would improve over that measured when the cats’ heads were restrained. On the whole, the experimental data support this hypothesis. Cats localized auditory and visual targets with better accuracy with the head unrestrained, although not necessarily with better precision. As we have reported earlier (Populin and Yin 1998a), localization of auditory targets with the head restrained was generally less accurate than to visual targets, but accuracy, and to a lesser degree, precision improved with stimulus duration for targets of both modalities. Moreover, with the head unrestrained, auditory localization was nearly as accurate as visual localization.

**Comparison to other studies**

Aside from our previous study (Populin and Yin 1998a), there have been few comprehensive studies of sound-localization performance based on eye saccades in the head-restrained cat. Hartline et al. (1995) reported that eye saccades to a 50-ms duration broadband noise in two cats undershot the targets producing horizontal gains of 0.76 and 0.72 and vertical gains of 0.6 and 0.82. That accuracy was better than that found here with similar, but shorter, duration auditory stimuli (see Table 1, 15 ms); the average localization gains computed across our three cats for the 15-ms stimulus were 0.44 and 0.53 for horizontal and vertical targets, respectively. However, Hartline et al. (1995) gave no report on response variability or precision. Peck et al. (1995) found their sample of cats could make eye saccades to long-duration (0.25–1.5 s) auditory and visual targets restricted to the horizontal plane with an average localization gain of 0.56 and 0.54, respectively, indicating considerable undershoot for both auditory and visual stimuli. The accuracy for long-duration auditory stimuli found by Peck et al. (1995) was comparable to that produced by our three cats (mean gain = 0.56, Table 1), but our cats’ visual localization of long-duration targets (1,000 ms) was more accurate (mean gain = 0.84). Similar to our results in head-restrained cats, Yao and Peck (1997) reported that eye saccades in head-immobilized humans to visual and auditory targets within ±20° on the horizontal plane resulted in localization gains of 0.94 and 0.68, respectively, although stimulus duration was unspecified. Whittington et al. (1981) also reported that monkeys undershot auditory targets along the horizontal plane with the head restrained.

Head-unrestrained gaze saccades to auditory targets to our knowledge have not been measured in cats, but there have been several such studies in humans (Frens and Van Opstal 1995; Vliegen and Van Opstal 2004; Zahn et al. 1978, 1979; Zambon and Van Opstal 1981; Zambon et al. 1982) and monkeys (Jay and Sparks 1990; Whittington et al. 1981). In perhaps the experiment most comparable to ours, Frens and Van Opstal (1995) reported good performance in human subjects (horizontal and vertical gains more than ~0.8) for auditory and visual targets with 500-ms durations. In both humans and cats, accuracy declined as the auditory stimuli were shortened, particularly for targets in elevation. Yet on average, the cats were able to localize even the shortest auditory stimuli (15 ms) to within ~1° for targets in azimuth and to within 2–3° for targets in elevation. This performance is comparable, and perhaps even superior, to that produced by humans (Makous and Middlebrooks 1990) and the barn owl (Knudsen et al. 1979), the latter often considered the best sound localizer of all terrestrial animals (Knudsen 1981). When compared over similar ranges of targets, the localization accuracy of the cats was better than that found in a previous study of sound localization in the head-restrained cat. In that study, May and Huang (1996) found that for targets located within ±15° in azimuth and elevation, the cats underestimated target location by ~5° with 40-ms duration broadband noise targets. That performance is comparable to the head-restrained performance found here. One important difference in the experiments was that May and Huang (1996) used the head position of the cats as an indicator of apparent location, whereas we used gaze shift. The underestimation of location found by May and Huang (1996) could have been due to their cats making a gaze shift, rather than a head movement alone, to the target so that their eyes would have been positioned in the orbits more laterally toward the target than the head. Our preliminary analysis of the gaze shifts indicated that this is indeed the case in our cats (Populin et al. 2000).

Finally, fewer experiments have studied the differences in sound-localization performance between head-restrained and -unrestrained conditions, none of which used cats. In one instance, head-restrained eye saccades by humans to long-duration auditory targets were about equally accurate as head-unrestrained gaze saccades in both azimuth and elevation (Goossens and Van Opstal 1999). However, as in their previous report (Frens and Van Opstal 1995), the observers’ heads were not mechanically restrained, but rather they were instructed to hold their head steady while they made saccades to the targets. It is presently unclear whether such methodological differences in head-restraint affect sound localization.

**Cats undershoot auditory targets in the head-restrained condition**

We found that localization performance was substantially worse in the head-restrained condition relative to that in the head unrestrained for all stimulus conditions. This was particularly the case for short-duration stimuli. For example, the mean gain across cats (Table 1) for the 15-ms auditory stimulus in azimuth increased from 0.44 to 1.0 and the mean signed error (Table 2) decreased from −7.24 to 0.15° simply by freeing the head. A similarly large improvement in gain was observed for the 25-ms visual stimuli in azimuth with mean gains increasing from 0.55 to 0.91 and the mean signed errors decreasing from −4.62 to −1.21°. The improvement in accuracy produced by freeing the head was unexpected for these short stimuli (15 and 25 ms, for auditory and visual, respectively) because the sensory conditions were virtually identical in both head-restrained and -unrestrained conditions because these stimuli would have been extinguished well before the onset of a saccade or a movement of the head or pinnae. Yet it was precisely for these short stimuli where performance was dramatically different in the two conditions.

Localization precision was also different between the head-restrained and -unrestrained conditions. With the head unrestrained, there was in general an unexpected worsening (larger δ) of precision, particularly for short-duration auditory targets despite an improvement in accuracy. It is possible that with
head-unrestrained gaze shifts, the additional degrees-of-freedom afforded by independent eye and head contributions to the gaze shift could lead to a worsening of precision. It is presently unclear why precision worsens when the head is unrestrained, particularly for short-duration auditory targets.

One additional difference between the head-restrained and unrestrained experimental conditions was the presence of the additional hardware needed to restrain the head (see Methods). The head-restraint device would be expected to alter the acoustical cues to sound-source location, relative to the cues without the device, particularly for very high frequencies (>28 kHz) with wavelengths comparable to the dimensions of the device (12 mm). It is possible that these altered localization cues could be responsible for the poorer localization performance with the head restrained relative to unrestrained. However, the cats also produced poorer performance for visual targets with the head restrained, particularly with short-duration stimuli. This suggests that for auditory targets there would still be some contribution to the poorer performance due to restraining the head above and beyond that which might have been caused by altered acoustical cues.

The advantage, albeit small (see Tables 1 and 2), of increased stimulus duration for localizing visual and auditory targets with the head unrestrained was expected based on the availability of dynamic location information as the eyes and head move (e.g., Wightman and Kistler 1999). Such dynamic information would not be available in the same way for auditory targets when the head was restrained because the cues for localization are in head-centered coordinates. However, short-latency, goal-directed movements of the pinnae toward the sound source are common in the head-restrained cat (Populin and Yin 1998b). Because such movements have been shown to affect the sound-localization cues (Young et al. 1996), this could be a factor in the improvement in localization accuracy with duration in the head-restrained condition. For the most part, only modest improvements in accuracy were seen in the head-unrestrained condition as stimulus duration increased because the performance was good to begin with for short durations. Although the improvements in accuracy with increasing stimulus duration were small with the head unrestrained, there were no apparent differences between the magnitudes of improvement seen for visual localization compared with auditory localization. This may be because in both visual and auditory conditions, the cues used to localize change dynamically and can be updated as the eyes and head move. Alternatively, another reason for the improvement with duration for both head-restrained and unrestrained conditions is that the short-duration tasks have a memory component because the targets were extinguished prior to the onset of the eye or gaze saccade, whereas the long-duration tasks do not. Moreover, there was no evidence suggesting that cats learned to take advantage of new strategies for using the localization cues by freeing the head (Fig. 5). In all, however, the localization of auditory targets was more accurate with the head unrestrained compared with restrained at any stimulus duration.

We believe that the undershooting with the head restrained is due to the unnatural sensory-motor conditions produced by restraining the head and not by a mechanical bias. First, all target locations in this study were within the oculomotor range of the cat (±25°) (Guitton et al. 1980). Second, our cats were able to accurately (gains near 1.0 in Table 1 and signed errors near 0.0° in Table 2) make eye saccades to each of the locations when presented with long-duration visual stimuli, demonstrating that mechanical limitations of the oculomotor system were likely not the cause for the underestimation of the sound sources.

Moreover, it is unlikely that the undershooting reflects a behavioral response bias, for example, that the cats may have learned to make eye saccades only as much as they needed to obtain a food reward. First, the sizes of the reward windows for auditory trials were often varied, so a consistently undershot target might or might not be rewarded depending on the window size. Second, in the control experiments when the target positions were shifted by 4.5° (to locations never associated with a visual stimulus), we have previously shown that the cats’ eye saccadic responses were also shifted by approximately the same amount, but the absolute target locations were still underestimated (e.g., Fig. 10 of Populin and Yin 1998a). We’ve added here that gaze saccades to these shifted targets were as accurate as to the standard target locations. Third, the cats were routinely presented with a large variety of possible tasks and stimuli, randomly intermixed. In fact, some of the stimuli were designed to elicit auditory spatial illusions, such as the precedence effect (Tollin and Yin 2003b), and the cats performed consistent with expectations for these stimuli, yet they still undershot. Fourth, if the undershoot were a behavioral bias, we might not expect the degree of undershoot to change with stimulus duration, yet it did. Fifth, the cats still underestimated targets with the head restrained after they had been exposed to the head-unrestrained condition, where they localized the targets accurately. Finally, the undershooting was not an artifact of the method by which initial and final gaze position was computed (see Populin and Yin 1998a, pg. 2150).

Possible mechanisms for undershooting in the head-restrained condition

Producing eye or gaze saccades to auditory or visual targets require that the spatial location of the target be estimated with respect to the current position of the eyes, head, and body. Only in this way can motor commands be generated to produce the appropriate combinations and magnitudes of movements of the eyes, head, and body necessary to acquire the target. When the head is held restrained, this naturally upset the “normal” mode of responding via combined eye and head movements. The fact that there is a systematic relationship between the position of the eyes in the head during an eye saccade and the activity of the muscles in the neck of the cat even when the head is restrained (Guitton et al. 1980; Vidal et al. 1982) demonstrates the tight coupling of eye and head movements in this species. Given that the oculomotor range of the cat (±25°) is small relative to primates (approximately more than ±50°), head movements would be required for cats to orient toward most targets. In agreement with this, although beyond the scope of this paper, with the head unrestrained, our cats virtually always moved their heads toward the target even for the smallest of gaze saccades, suggesting that head movement is an indispensable part of the orientation response of the cat.

Because of the relationship between eye position and neck muscle activity cited in the preceding text, it is possible that the position of the eyes and the associated neck muscle activity...
during a head-restrained eye saccade may alter the proprioceptive information about the position of the head leading to an illusory shift of the target location. In support of this hypothesis, proprioceptive information from the neck has been shown, by vibrating the neck muscles, to alter an observers’ perception of the location of visual (Biguer et al. 1988; Taylor and McCloskey 1991) and auditory (Lewald et al. 1999) targets. Consistent with this, Corneil and Anderson (2004) have recently demonstrated that vibrating the dorsal neck muscles of monkeys causes a displacement of memory-guided saccades to remembered visual targets. The vibrations in each of these studies are believed to stimulate the muscle-spindle afferents resulting in a proprioceptive signal that those muscles have lengthened. Thus vibrating the appropriate neck muscles gives the perceptual illusion of a head turn contralateral to the stimulated muscle. Using the neck-vibration technique, Lewald et al. (1999) showed that stimulation of the neck muscles on one side caused in some, but not all, subjects a shift in the perceived location of dichotic stimuli with interaural level disparities toward the side of stimulation. This finding corresponds to what would be expected had the head actually turned away from the side of neck stimulation (Lewald and Ehrenstein 1998). Lewald et al. (1999) suggested that there might be a direct influence of the neck proprioceptive information on the neural mechanism responsible for transforming the coordinates of the central representation of the auditory spatial location of that target from a head-centered to a body-centered frame of reference. In our head-restrained condition studied in this paper, if either the torque resulting from an attempted head movement toward the target produces a proprioceptive signal (via gamma efferent bias) or if an efference copy signal of the motor command to move the head were similar to that induced by vibration of the neck contralateral to the target, then the apparent target for an eye saccade would be shifted medially resulting in an underestimation of the actual target location.

Further supporting this hypothesis, Goossens and Van Opstal (1999) demonstrated using a double-step saccade paradigm that accurate eye and gaze saccades to auditory targets by humans requires the use of a head-position signal. In their model, the head-position signal may be computed from the vestibular system, proprioceptive feedback from the neck, or an efference copy of the motor commands to move the head. But when the head is physically restrained, it is likely that this signal is distorted. While the vestibular system may correctly indicate that the head did not move, the efference copy of the intended head movement may indicate that it did, and/or the cat may have actually attempted to move the head resulting in ambiguous proprioceptive information. A distorted head-position signal would be expected to lead to systematic alterations of apparent source location. Like Lewald et al. (1999), Goossens and Van Opstal (1999) also proposed that a signal about head movement/position acts at the level of the sensory input, possibly the superior colliculus. Indeed, stimulation of the afferent nerves of the neck muscles in cats has demonstrated that these project to the intermediate to deeper layers of the SC (Abrahams and Rose 1975). Many of these neurons in the cat are sensitive to both auditory and visual stimuli (Populin and Yin 2002), the neural responses of many of these SC neurons can also be modulated by the position of the head in the cat (Jay and Sparks 1984; Populin et al. 2004). Moreover, electrical (Roucoux et al. 1980) stimulation of the SC in head-unrestrained cat results in conjoint movements of the eyes and the head that were goal directed. Hence, at the SC, there may be a convergence of auditory spatial information with proprioceptive information about the position of the head and the eyes in the head and/or an efference copy of the motor commands for eye and head movements. It is conceivable that the auditory receptive fields of SC neurons could also be shifted by head position, real or illusory.

An alternate hypothesis for the underestimation of the targets with the head restrained is that the magnitudes of the eye saccades produced when the head is restrained are reduced by the amount that the head would have contributed to the gaze saccade if the head had been free to move. This hypothesis follows from the models of Freedman et al. (1996) and is supported by the experiments of Roucoux et al. (1980) and Freedman et al. (1996), who found that electrical stimulation of sites in the superior colliculus, which produce large gaze saccades, drove the eyes to approximately the same (i.e., goal-directed) orbital position regardless of whether the head was restrained or unrestrained. It is also consistent with the tight coupling of eye position and neck muscle activity in the cat (Guitton et al. 1980; Vidal et al. 1982) and the strong propensity of cats to make head movements even for the smallest of gaze saccades (e.g., Guitton et al. 1984). In our behavioral experiments, an underestimation of the target might occur because the eyes were only programmed to move to a specific orbital position that when combined with a head movement would have brought the gaze position into alignment with the target. But because the head was restrained, the final orbital position of the eye undershoots the target. In accordance with this hypothesis, Guitton et al. (1984) demonstrated that cats, expecting to make gaze saccades to visual targets located beyond 10° in azimuth, produced eye saccade amplitudes of only ~12° in a condition where their heads were unexpectedly restrained just prior to the onset of the gaze shift. That is, the cats undershot the target even though the oculomotor range of the cats (approximately ±25°) would have permitted substantially larger-amplitude eye saccades. These findings are consistent with the undershooting we have observed when the heads of the cats were restrained. This hypothesis, however, appears to require that the mechanism by which gaze saccades are programmed, in terms of the relative contributions of eye and head movements, does not know whether or by how much the head had moved. Both this and the hypothesis discussed in the earlier section require that proprioceptive information about head position is either not taken into account or that the proprioceptive feedback is inappropriate when the head is restrained. Our data do not allow us to definitively test these hypotheses.

In summary, it is of interest to obtain the best estimate of the perceptual abilities of the animals used for physiological experiments, as these estimates are necessary to constrain hypotheses and models of the neural bases by which sound-source location is encoded in the CNS. Critical is the relationship between the locations of sounds and the accuracy and precision of the behavioral reports of location by the cats. This is important because it allows for the direct comparison between the acoustical cues to sound location, the animals’ localization performance and the neural representation of space. While a head-restrained preparation may be convenient for chronic electrophysiology, we have shown here that local-
ization performance is different from that obtained when the head is unrestrained, even when the stimulus conditions are virtually identical (i.e., short-duration stimuli). This is not to say that performance measured in the head-restrained condition is “wrong” but rather the unnatural act of restraining the head may alter the natural sensory-motor conditions leading to illusory shifts in the target locations, particularly for auditory stimuli. Future studies should take into account such differences.

ACKNOWLEDGMENTS
We acknowledge the assistance of J. Sekulski and R. Kochhar for help with computer programming and J. Hudson for help with animal training and data analysis. Special thanks to Prof. Michele Basso and Dr. Michael Dent for commenting on earlier versions of the manuscript.

GRANTS
This work was supported by National Institutes of Deafness and Other Communication Disorders Grants DC–00116 and DC–02840 to T.C.T. Yin and Gilkey R, Good M, and Ball J.

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