Simultaneous comparison of two sound localization measures

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ABSTRACT

Almost all behavioral studies of sound localization have used either an approach-to-target or pointing/orienting task to assess absolute sound localization performance, yet there are very few direct comparisons of these measures. In an approach-to-target task, the subject is trained to walk to a sound source from a fixed location. In an orienting task, finger, head and/or eye movements are monitored while the subject’s body is typically constrained. The fact that subjects may also initiate head and eye movements toward the target during the approach-to-target task allows us to measure the accuracy of the initial orienting response and compare it with subsequent target selection. To perform this comparison, we trained cats to localize a broadband noise presented randomly from one of four speakers located ±30° and ±60° in azimuth. The cat responded to each sound presentation by walking to and pressing a lever at the perceived location, and a food reward was delivered if the first attempt was correct. In tandem, we recorded initial head and eye orienting movements, via magnetic search coils, immediately following target onset and prior to the walking response. Reducing either stimulus duration or level resulted in a systematic decline in both measurements of localization performance. When the task was easy, localization performance was accurate for both measures. When the task was more difficult, the number of incorrect (i.e., wrong selection) and no-go (i.e., no selection) responses increased. Interestingly, for many of the incorrect trials, there was a dissociation between the orienting response and the target selected, and for many of the no-go trials, the gaze oriented towards the correct target even though the cat did not move to it. This suggests different neural systems governing walking to a target as compared to unconditioned gaze orienting.

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1. Introduction

The ability to localize sounds is a major function of the auditory system and crucial for many mammals to survive in the wild. Finding food and avoiding danger requires collecting precise and timely sensory information and executing appropriate motor commands. Naturally, different sounds will elicit different phonotaxic responses, e.g., an unexpected sound will elicit a reflexive head and/or eye orienting response and, contingent upon circumstances, an approach or flee response. These behavioral responses, specifically orienting and approaching, have been exploited in numerous studies of sound localization. Though both behaviors have effectively served as measures for assessing auditory localization ability, previous studies have demonstrated contradictory results implementing the two measures. For example, when unilaterally lesioning or inactivating the primary auditory cortex (A1), Kavanagh and Kelly (1987) and Malhotra et al. (2004) observed contralateral localization deficits with the approach-to-target task, whereas Beitel and Kaas (1993) reported no change in head-orienting responses. In a similar cortical inactivation study conducted with ferrets, Smith et al. (2004) observed degraded approach-to-target performance yet no change in the initial head-orienting behavior. However, when Nodal et al. (2008) compared the two localization behaviors in ferrets, they found the head-orienting and the conditioned-approach responses to be closely related. These contradictory findings suggest that the approach-to-target responses and the orienting responses may be mediated by different neural pathways, which would explain why the two responses can occur independently under certain conditions.

The orienting response to visual and auditory input consists of coordinated movements of the head and eyes. In the present study, both head and eye movements were recorded before the cats walked to a sound source. In the previously mentioned studies, the orienting responses were measured via head movement. Importantly, a progressive undershooting has been reported for head
movements to acoustic targets with increased speaker eccentricity (Beitel and Kaas, 1993; May and Huang, 1996), and a direct comparison with the cat’s gaze movements (i.e., eye in space resulting from combined head movement and eye saccade) has shown that the localization performance quantified by gaze movements is significantly more accurate than that of the head (Tollin et al., 2005; Ruhland et al., 2013). Here, we performed the first direct comparison of gaze orienting and approach-to-target performance acquired simultaneously for a wide variety of stimulus conditions. A noteworthy difference between our present study and previous localization studies using gaze movements is that the cat’s behavior is rewarded on their approach-to-target responses, not on their gaze movement.

Although there is ample evidence to support the involvement of both auditory midbrain and cortex in sound localization, to what extent they are responsible for reflexive orientation and approach-to-target behavior, respectively, remains unclear. Here, we trained cats to localize auditory targets in a self-initiated approach-to-target paradigm while we concurrently recorded their head and eye positions. We examined the effects of manipulating the level of difficulty on both localization accuracy of the initial orienting response and approach-to-target performance in an effort to identify conditions in which the two localization behaviors may operate independently.

2. Methods

2.1. Subjects and surgery

Three adult female cats were implanted with a stainless steel head post and scleral search coils (S170012A7-FEP, 137 Alan Baird Industries, Ho-Ho-Kus, NJ) in their eyes under general anesthesia and aseptic surgical conditions. The eye-coil wires were threaded subcutaneously up to the head post, soldered to connectors and secured with dental acrylic. A third coil-loop, for monitoring head movement, was oriented coronally and embedded directly into the dental acrylic encasing the head post. Anesthesia was induced with ketamine (20 mg/kg) and maintained with isoflurane gas (1–2% in O2) during surgery. Postoperative treatment consisted of an analgesic ketoprofen (2.0 mg/kg) and penicillin to prevent infection. All surgical and experimental procedures were approved by the University of Wisconsin Animal Care and Use Committee and in compliance with National Institute of Health guidelines for animal use.

2.2. Experimental setup and stimuli

All behavioral tasks were carried out on a platform (Fig. 1) in a dimly lit sound-attenuated recording booth (2.2 × 2.5 × 2.5 m) with acoustic foam-lined walls and ceiling (10.2 cm Sonex, Illbruck Co.). Four speakers (RadioShack model 40–1310B, Fort Worth, TX) were arranged horizontally, along an arc 80 cm in radius, in the frontal hemi-field at ±30° and ±60°, within the limit of motor control for gaze saccades. An LED (2.0 mm red light emitting diode, λ_max = 635 nm) was suspended over the center of each speaker, and a central LED was positioned straight ahead (0°, 0°). Levers and food spouts were available at each speaker. Since the eye and head coil measurements are only valid when the head is positioned near the center of the field coils, it is also necessary to monitor the position of the head at the start of the trial and ensure that it is within acceptable limits. For this purpose, a sensor was placed above the center of the platform, directed downward to the start position. The magnetic search coil (CNC Engineering, Seattle, WA) technique (Fuchs and Robinson, 1966) was used to monitor head and gaze (eye-in-space) positions, and the analog outputs of the coil system were recorded at a sampling frequency of 500 Hz.

Acoustic targets were broadband (25 kHz) noise, presented from 1 of the 4 speaker locations, of various durations (25, 40, 100, 500, 1000 ms) and sound levels (–10 to 30 dB SPL). Stimuli were generated using a Tucker–Davis Technologies III system (Alachua, FL) at a sampling frequency of 50 kHz.

2.3. Behavioral paradigm

Cats were trained by operant conditioning to perform the localization tasks. Two of the three cats (cat 21 and cat 32) had participated in gaze-orienting sound localization tasks prior to this study while the third cat was previously untrained. None had any experience with the approach-to-target task. In the present study, the cat initiated each trial by positioning its body within the acceptable range of the overhead sensor while pointing its head to the central LED presented from straight ahead (0°, 0°) within an acceptance window of 12–14° in azimuth and 12–15° in elevation for a variable period of time (600–2500 ms). Random trial-by-trial variation in fixation time prevented the cat from predicting the onset of target presentation. Once the LED was extinguished, the acoustic target was simultaneously presented and the cat was required to indicate its response by walking to and pressing a lever at the perceived location to receive a food reward. The cat initiated the next trial by walking back to the start position and repeating these steps. Thus the training was self-paced and terminated when the cat ceased to perform the task. To avoid bias against any particular speaker location, an incorrect response was followed by a single correction trial (i.e., same stimulus presented from same location). Correction trials were rewarded if targets were correctly selected but were not included in the analysis. This protocol also has the advantage of avoiding possible bias from experimenter intervention during the reward phase. The LEDs aligned with the speakers were occasionally paired with auditory targets to provide bimodal targets during the early phases of training and coil calibrations.

A unique aspect of the present study is to couple recordings of head and gaze orientation immediately before and after the presentation of the acoustic stimulus using the magnetic search coil technique. Importantly, the head and gaze signals were not linked to any behavioral measure so the reward was not contingent upon
head or gaze behavior. We feel that in this regard any head or gaze movement was a natural response to the cat’s effort to localize the sound source.

Eye coils were calibrated with a behavioral procedure (Populin and Yin, 1998) that relies on the natural instinct of the cat to look at an unexpected light source that appears in the visual field. When the cat visually fixated the LED, the output of the coil system was recorded. This was repeated for each LED location. The horizontal and vertical components of the final eye positions were fit separately with linear first-order regression equations. The coefficients obtained from the fitting procedure were used to convert the voltage output of the coil system to degrees of visual angle. The head was calibrated in a similar fashion except we manually aligned the head with each LED location. Coefficients of determination (i.e., $R^2$) for fits exceeded 0.9. Control experiments with a dummy coil indicated that the calibration was relatively pitch-invariant and the presence of the experimenter in the recording booth did not alter the calibration.

2.4. Data analysis

For the approach-to-target measurement, we recorded which lever was pressed by the animal (i.e. the perceived location of the speaker) and converted the responses into percentages (i.e., percent correct, incorrect, and no-go) for each parameter tested. With the exception of the correction trials, all trials were included, even if the cat did not approach any target (i.e., no-go trials), as long as an acoustic target was triggered. Walking latency was measured as the point in time in which the animal leaves the start position, i.e., no longer breaking the sensor, in pursuit of the presented target (“sensor out” time indicated in Fig. 2A).

For the head/gaze orienting measurement, we used a velocity criterion (Populin and Yin, 1998) to determine the end of fixation (onset of head or gaze movement) and return to fixation (end of head or gaze movement) by calculating the time at which the magnitude of the velocity exceeded or returned, respectively, to 2 standard deviations of the mean velocity computed during the fixation of the initial LED. Latency of the orienting response was measured as the time between target onset and the end-of-fixation, i.e., the time at which the gaze or head shift began relative to target onset. Trials with either head or gaze onset latencies greater than 2000 ms were excluded from the analysis.

Localization performance was measured by comparing gaze shift (i.e., final position relative to initial position) with motor error (i.e., target location relative to initial gaze position). The gaze shift describes the angular magnitude and the direction of the saccade. The motor error describes the magnitude of the gaze shift needed to acquire the target given the initial position. To quantify the localization performance across all target locations, a linear function was fit to the data, and its slope, which was referred to as gain (Tollin et al., 2005), indicates the accuracy with which the cat localized the targets. A gain of 1 indicates that, on average across all trials, the cat oriented to the actual target locations. A gain <1.0 indicates undershooting of the target locations. The standard deviation of the residuals of the fitted function (b), which is the inverse of precision, was computed to measure the distribution of the behavioral responses. This value provides a numerical estimate of the precision (i.e., consistency) of the localization responses (Moore et al., 2008). Larger values indicate more scatter of the localization responses. Statistical bootstrapping (Efron and Tibshirani, 1986) was used to obtain an estimate of the 95% confidence intervals of accuracy (gain) and precision (b). We also computed head shift gain for comparison to gaze shift.

3. Results

Three domestic cats were trained to perform the task. The two experienced cats (cat 21 and cat 32), who were previously trained on a gaze shift task, learned the task in approximately one month. The naïve cat (cat 39) learned the task in two weeks. The results presented here are based on the analysis of 5898 approach-to-target trials with clear head and gaze traces (2,404, 1,067, and 2427 for cat 21, 32, and 39, respectively).

An important aspect of this study is the ability to compare the initial gaze shift with the location of the speaker that the cat walks to and chooses to obtain a reward. By placing the walking platform within the Helmholtz field coils and requiring the head of the cat to be within the acceptable range, we are able to monitor the reflexive gaze shift of the cat immediately after target onset prior to the walking. The cats appear to know that when their head or body is not in the correct position, they must move one way or another until the LED comes on to signal that their position is correct (see video in Supplementary material). The green vertical line labeled “sensor out” in Fig. 2A marks the point in time at which the head was no longer in the central start position as determined by the movement of the head out of the sensor as the cat started walking to the target. Fig. 2A shows the horizontal (blue) and vertical (red) gaze shifts in response to a target (30 dB SPL, 100 ms duration) presented from −60° in azimuth. The target was turned on at time 0 marked by the vertical magenta line. The final gaze position as determined by the return to fixation (the point at which the velocity returned to within 2 SD of the velocity during steady fixation) is marked by the dashed lines for both the horizontal and vertical components of the gaze shift. In this case there is an 8° undershoot of the target at −60°. Fig. 2B shows the final gaze positions for 699 trials for cat 21 in localizing 30 dB SPL noise bursts of all durations presented from the four target positions, with each position coded by a different color. The final gaze positions cluster about the appropriate target positions for all four targets with an undershoot to the more eccentric targets.

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.heares.2014.08.007.

![Fig. 2. Example of gaze movement and final gaze positions. (A) Horizontal and vertical gaze movement to a 30 dB SPL noise of 100 ms duration presented from −60° in azimuth. The final gaze position is marked by the dashed lines for both the horizontal and vertical components of the gaze shift. (B) Final horizontal and vertical gaze positions to 30 dB SPL noise of all durations for all target locations at 60° left (blue), 30° left (green), 30° right (red), and 60° right (teal).](http://dx.doi.org/10.1016/j.heares.2014.08.007)
At the highest sound level used (30 dB SPL), approach-to-target performance was consistent across all target locations and durations with predominantly correct responses. Fig. 3A shows the approach-to-target performance reflected as percentage of correct, incorrect, and no-go responses to 30 dB SPL targets for each speaker location at all durations for all three cats. The plot shows high percent-correct values (mean percent correct is 86%, incorrect 11% and no-go 3%) and left-right symmetry of the responses. The corresponding gaze shifts are plotted as a function of motor error (target location relative to initial gaze position) for cat 21 in Fig. 3B. Accuracy is summarized by gain or the slope of the linear regression (solid/red line). The localization gains derived for the three cats were >0.75 (gain = 0.77, 0.75, and 0.78 for cat 21, 32, and 39, respectively). Thus, for 30 dB SPL targets, localization performance was relatively accurate for both measures.

Fig. 4 shows similar effects of sound level and duration on approach-to-target and gaze orienting responses for all three cats. Fig. 4A shows the percent of correct approach-to-target responses for each duration at each sound level tested. Each duration is plotted in a different color. In general, increasing either stimulus level or duration resulted in improved approach-to-target performance. Stimulus duration appears to have had a more pronounced effect on cat 32’s performance as compared to the other two cats. In Fig. 4B, the gaze response accuracy (gains) and the associated 95% confidence intervals are plotted for each stimulus duration as a function of sound level for all three cats. For all cats, the gains were near chance at 0 or -10 dB SPL and then rose to plateau at the highest sound levels tested. At the lowest levels, the sounds are likely to be at or near detection threshold. In general, at any given level, the gains for short duration targets were lower than for the longer duration targets, with little difference between the 500 and 1000 ms durations. Fig. 4C shows the precision for each of the durations as a function of sound level. For all three cats, precision improved with increasing sound level and with increasing duration, especially with cats 32 and 39. Overall, sound level appears to have had a more consistent effect than duration on both measurements.

Fig. 5 compares approach-to-target and gaze orienting responses for cat 21. Fig. 5A plots all the approach-to-target responses (i.e., lever selections, y-axis vs. true target locations, x-axis) for the 30 dB SPL (top), 10 dB SPL (middle), and 0 dB SPL (bottom) targets, and the points are plotted with some artificial jitter on both the ordinate and abscissa to make the data points more visible. The data points deviating from the diagonal (dashed line) represent incorrect selections, and the points along Selection 0 indicate that no selection was made (i.e., no-go trials). As expected, there are more incorrect and no-go selections with decreasing sound level. All corresponding gaze orienting responses are plotted in Fig. 5B. The gaze shifts (where the cat looked) are plotted as a function of motor error (angle between actual target location and initial gaze position) for each sound level. Performance of both the approach-to-target and gaze orienting response declined with decreasing sound level.

The gaze orienting responses of the correct and no-go approach-to-target trials are plotted in Fig. 6. Fig. 6A plots the gaze shifts of all the correctly selected trials as function of motor error. The gain and R-value of the correlation (r1) are indicated for each sound level. The high values of r1 indicate a high correlation between where the cat looked and the target location for all three sound levels. This means that correct selections were typically preceded by correct orienting responses. Fig. 6B plots the gaze shifts of all the no-go trials as a function of motor error. For the no-go trials, the gain and regression value (r2) were high for the 30 dB SPL targets (top) but declined with decreasing sound level. The high gain and R-value indicate that, on average, for these high level stimuli the cat oriented correctly but, for unknown reasons, did not approach any target (i.e., no-go). In contrast, for 0 dB SPL targets (bottom), the gain and R-value were much lower, indicating that the cat did not approach any target perhaps due to uncertainty of the target’s location or inability to hear the stimulus (low r2).

The gaze orienting responses of the incorrect approach-to-target trials are plotted in Fig. 7. Gaze shift was plotted as a function of either motor error (Fig. 7A) or incorrect selection (selection angle relative to cat’s initial gaze position; Fig. 7B). The trials are color coded by the location of the target. For the 30 dB SPL targets (top row), the rightmost cluster of points (turquoise) represent targets at +60° with which the cat oriented to and approached +30°. This is confirmed by the same clusters of points.

Fig. 3. Localization performance for the highest sound level tested (30 dB SPL targets of all durations). (A) Percentage of correct, incorrect, and no-go approach-to-target responses for each speaker location for cat 21 (top), cat 32 (middle), and cat 39 (bottom). Performance was consistent across four target locations. (B) Horizontal gaze shift as a function of motor error (target location relative to initial gaze position) for cat 21. Accuracy is summarized by gain or the slope of the linear regression (solid/red line). Gain < 1.0 indicates undershooting of the target location. δ is the residual error after regression and indicates response precision (Tollin et al. (2005) J. Neurophysiology. 93:1223–1234).
in Fig. 7B, showing the selection angle for these same trials. Similarly the red cluster in Fig. 7A are targets at \(+30^\circ\) with which the cat oriented to the correct target \(+30^\circ\) but approached the wrong one \(+60^\circ\) as shown in Fig. 7B. Thus for some of these incorrect trials, the cat looked to the wrong target and subsequently selected the same incorrect target (turquoise and blue targets) while for others the cat looked at the correct target location but selected the other speaker on the same side (red and green targets). The same trend is also evident at 10 dB SPL (Fig. 7A, middle row). For the 0 dB SPL targets (Fig. 7A, bottom), however, the points for each target location are highly scattered and show that the cat often looked to the hemi-field opposite to the target, which never happened for 30 dB

![Fig. 4](image)

**Fig. 4.** Effect of sound level and duration on approach-to-target performance and the corresponding gaze orienting responses. (A) Percent of correct approach-to-target responses for each stimulus duration at each sound level tested. (B) Gains of gaze shift for each stimulus duration at each sound level tested. (C) Delta \(\delta\) of gaze shift for each stimulus duration at each sound level tested. \(\delta > 0\) indicates scattering of localization responses.

![Fig. 5](image)

**Fig. 5.** Comparison of all approach-to-target and gaze orienting responses to 30 dB SPL (top row), 10 dB SPL (middle row), and 0 dB SPL targets (bottom row) across all durations. (A) All approach-to-target responses. Points off the diagonal represent incorrect selections. Data are plotted with some artificial jitter for illustration purposes. (B) All corresponding gaze orienting responses of (A). Gaze shift plotted as a function of motor error (target location relative to initial gaze position at target onset). Accuracy declines at low levels.

![Fig. 6](image)

**Fig. 6.** Gaze orienting responses of correct and no-go approach-to-target trials. (A) Gaze orienting responses of correct trials. At all three sound levels, R-values indicate a high correlation between where the cat looked and target location. (B) Gaze orienting responses of no-go trials. High correlation for 30 dB SPL trials. These trials represent cases in which the cat oriented correctly but did not approach any target.
Fig. 7. Gaze orienting responses to 30 dB SPL (top row), 10 dB SPL (middle row), and 0 dB SPL targets (bottom row) for incorrect approach-to-target trials. (A) Gaze shift as a function of motor error. (B) Gaze shift as a function of incorrect selection angle (selection angle relative to cat's initial gaze position at target onset). The target angles are indicated by the colors: blue (−60°), green (−30°), red (+30°) and turquoise (+60°).

SPL targets. This suggests that the 0 dB SPL sound level was at or near the cat's threshold.

Performance analyzed by combining the two approaches is summarized for the three cats in Fig. 8. Gains of the gaze orienting responses are plotted for all approach-to-target outcomes at each sound level tested. The correct trials (blue) show the highest gain values for orienting responses across all levels for all three subjects. This indicates that even at low sound levels, the correct trials were associated with an accurate perception of the targets. Accuracy improved for the incorrect and no-go trials with increasing sound level. This indicates that at higher sound levels, the cats most likely localized the sound correctly but for whatever reason did not approach the correct location. These patterns were observed in all three cats.

Since several studies have used head movement to judge localization performance, it is of interest to compare gaze and head movement in our present study where the cat was rewarded on approach-to-target rather than either gaze or head movement. Fig. 9 compares gaze and head localization accuracy for all 3 cats. In Fig. 9A, the gaze response accuracy (gains) and the associated 95% confidence intervals are plotted for each stimulus duration as a function of sound level for all three cats. Each duration is plotted in a different color. For all cats, the gains were near chance at 0 or −10 dB and then rose to plateaus at the highest sound levels tested. In general, at any given level, the gains for short duration targets were lower than for the longer duration targets, with little difference between the 500 and 1000 ms durations. Head gains and associated 95% confidence intervals are plotted in Fig. 9B. For all three cats, gains values were lower for the head than for the gaze for sound levels ≥0 dB (i.e., well above threshold). Additionally, response patterns of the head were congruent with those of the gaze, i.e., similar trends with level and duration were apparent. If we combine all durations and compare the gaze and head accuracy (Fig. 9C), for all levels greater than threshold, gains of the gaze were above those of the head. At 30 dB SPL, the mean gain of the gaze was 0.77 while the mean gain of the head was 0.59, so the gaze movement had on average a 23.4% undershoot while head movement was only 76.6% of the gaze movement. Therefore, gaze movements are more accurate than head movements in sound localization, and we have used gaze rather than head movements in all of our localization analyses.

4. Discussion

Approach-to-target and orienting tasks have been used interchangeably to study sound localization behavior in the cat model for decades. Casseday and Neff (1975), Jenkins and Masterton (1982), Jenkins and Merzenich (1984), and Malhotra et al. (2004) assessed sound localization ability by implementing the approach-to-target task. A head-orienting task was used by others (Thompson and Masterton, 1978; Beitel and Kaas, 1993; May and Huang, 1996) to monitor behavioral performance.

Studies on the neural mechanisms of sound localization have identified key structures in the brainstem and auditory cortex. Physiological studies have confirmed brainstem involvement in many fundamental features of sound localization and have shown the role of the superior olivary complex (SOC), inferior colliculus (IC) and superior colliculus (SC) in mediating orienting responses of the head, eyes, and external ears (Rose et al., 1966; Goldberg and Brown, 1969; Boudreau and Tsuchitani, 1970; Stein and Clamann, 1981; Yin and Kuwada, 1983; Yin et al., 1987; Yin and Chan, 1990; Lomber et al., 2001; Tollin and Yin, 2002a, 2002b; Populin and Yin, 2002). In addition, there are extensive physiological and behavioral studies supporting cortical involvement, specifically the primary auditory cortex, in sound localization. Most compelling are the studies that have shown dramatic deficits in sound localization behavior following lesions or inactivation of A1 (Whitfield et al., 1972; Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984; Beitel and Kaas, 1993; Malhotra et al., 2004; Malhotra and...
Lomber, 2007; Lomber et al., 2007; Lomber and Malhotra, 2008; Nodal et al., 2010). However, results were not always consistent and varied with the behavioral task used to assess localization ability. For example, subsequent to unilaterally inactivating A1, contralateral localization deficits were observed with the approach-to-target task (Malhotra et al., 2004) but not with the head orienting task (Beitel and Kaas, 1993). In a similar cortical inactivation study in ferrets, Smith et al. (2004) also observed degraded approach-to-target performance and yet no change in head-orienting behavior. These findings suggest that different neural circuits may be responsible for voluntary localization and reflexive orientation as suggested by Thompson and Masterton (1978). In addition, the latency for the orienting movements of the pinna (25–35 ms; Populin and Yin, 1998), head and eyes (49.5 ms; Tollin et al., 2009) and the evoked pinna movements via electrical stimulation of the SC in bats (16–21 ms; Valentine et al., 2002) and the mean latency to acoustic stimuli in the SC of cats (17.7 ms; Populin and Yin, 2002) seem too short to require cortical processing.

In our previous studies (Tollin et al., 2005; Ruhland et al., 2013), we have monitored both head and gaze orienting movements with the head unrestrained and argued that localization accuracy is best represented by the gaze because head movements to auditory targets were less consistent and tended to undershoot the final gaze positions by −10–30% with a mean of 22%. However, a confound in our previous studies is that the rewards were contingent on accurate gaze movement, not head movements. Theoretically, the results might be different if we did not reward the cat for accurate gaze movement. However, the present results show that when the reward contingency was correct lever pressing and did not depend on either head or gaze movements, gaze movements were still more accurate than head movements with undershooting of the head when the cat naturally responded to the sound immediately after onset (Fig. 9). In addition, the degree to which the head gain was less than the gaze gain was essentially identical in this study (23.4%) to the mean found in our previous studies (22%, Ruhland et al., 2013), suggesting that the cats’ performance is not influenced by the behavior being rewarded.

In the current study, we implemented both localization tasks and performed a simultaneous, trial-by-trial comparison of the two responses. By varying sound level and duration we found conditions in which the two localization behaviors can operate independently. Nodal et al. (2008) compared the two localization behaviors in ferrets and reported that, despite varying the level of difficulty, head orientation invariably preceded the walking response, which led them to suggest that both initial head and conditioned approach responses rely on the same neural processing strategies. The lack of effect of stimulus duration and level (Nodal et al., 2008) may however be explained by the findings of Gai et al. (2013) as they observed that, in azimuth, neither sound level nor duration had a significant effect on localization accuracy except at near-threshold levels. In general, there seems to be a good correlation between the gaze orienting and approach-to-target responses for easy-to-localize stimuli, and our results in the cat were similar to those reported for ferrets in that the correct selections were typically preceded by accurate orienting responses. However, at near threshold levels, we observed cases where the cats looked to one target and approached another as well as cases where the cats oriented correctly but approached the wrong target. The occurrence of these trials increased with decreasing sound level. The dissociation between orientation and target selection for near-threshold stimuli suggest that the neuronal mechanisms for gaze orienting are not identical to those for approach to target. The cortical inactivation or lesion results suggest that the cortex is important for the latter while we suggest that the brainstem may be crucial for the former behavior.

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