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Differential Effect of Near-Threshold Stimulus Intensities on Sound Localization Performance in Azimuth and Elevation in Normal Human Subjects

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ABSTRACT

The ability of humans to localize sounds remains relatively constant across a range of intensities well above detection threshold, and increasing the spectral content of the stimulus results in an improvement in localization ability. For broadband stimuli, intensities near detection threshold result in fewer and weaker binaural cues used in azimuth localization because the stimulus energy at the high- and low-frequency ends of the audible spectrum fall below detection threshold. Thus, the ability to localize broadband sounds in azimuth is predicted to be degraded at audible but near threshold stimulus intensities. The spectral cues for elevation localization (spectral peaks and notches generated by the head-related transfer function) span a narrower frequency range than those for azimuth. As the stimulus intensity decreases, the ability to detect the stimulus frequencies corresponding to the spectral notches will be more strongly affected than the ability to detect frequencies outside the range where these spectral cues are useful. Consequently, decreasing the stimulus intensity should degrade localization in both azimuth and elevation and create a greater deficit in elevation localization due to the narrower band of audible frequencies containing elevation cues compared to azimuth cues. The present study measured the ability of 11 normal human subjects to localize broadband noise stimuli along the midsagittal plane and horizontal meridian at stimulus intensities of 14, 22, and 30 dB above the subject's detection threshold using a go/no-go behavioral paradigm. Localization ability decreased in both azimuth and elevation with decreasing stimulus intensity, and this effect was greater on localization in elevation than on localization in azimuth. The differential effects of stimulus intensity on sound localization in azimuth and elevation found in the present study may provide a valuable tool in investigating the neural correlates of sound location perception.

Keywords: sound localization, intensity, human, psychophysics

INTRODUCTION

The three main cues used to compute the spatial location of acoustic stimuli are the interaural time/phase differences (ITD), interaural intensity differences (IID), and spectral cues. Localization ability improves as the stimulus frequency bandwidth increases and more binaural and spectral cues exist in the stimulus, resulting in better sound localization ability for broadband stimuli, such as clicks and noise, compared with tonal stimuli (see Middlebrooks and Green 1991; Blauert 1997). This improvement in localization ability can be attributed to the availability of both types of binaural cues across a broader frequency range, as well as the addition of spectral cues for stimuli with broad spectral bandwidths. Similarly, at the neuronal level more neurons in central auditory structures would be activated by broadband stimuli than by tonal stimuli, resulting in a larger activated population of spatially

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sensitive neurons that could contribute to the spatial computation of auditory stimuli.

Reducing localization cues can also be accomplished by decreasing the stimulus intensity of broadband sounds. Since humans are normally more sensitive to some stimulus frequencies than others, near detection threshold of broadband noise the energy at many frequencies (e.g., the high and low frequencies of the audible range) would not be detectable. This decreased performance has been observed for localization in azimuth at low intensities (Altshuler and Comalli 1975; Comalli and Altshuler 1976; Recanzone et al. 1998), but the effect of stimulus intensity on localization in elevation has not been thoroughly investigated.

The spectral cues resulting from the head-related transfer function (HRTF) are believed to be critical for localization in elevation (Wightman and Kistler 1989a, b; Carlile and Pralong 1994). Frequencies corresponding to the spectral notches and peaks in HRTFs change systematically with the stimulus location, and changes in the notch frequencies are elevation-dependent (see Middlebrooks and Green 1991). Although spectral notches are not the only elevation cues available to listeners, these high-frequency notches are likely to be more important than the non-notch cues. At low stimulus intensities, the stimulus energy at the frequencies corresponding to these notches could be near or below the detection thresholds of central neurons responding to these frequencies. Thus, the bandwidth of these spectral notches at detection threshold would increase as the stimulus intensity decreases, creating ambiguities as to the notch frequency and leading to a degraded localization ability in elevation.

Since interaural cues used in azimuth localization extend across a broader frequency range than the spectral cues used in elevation localization, greater deficits should occur for sound localization ability in elevation compared with that in azimuth at low stimulus intensities. In this study, we tested this prediction by comparing the ability of normal human subjects to localize broadband noise stimuli in both the horizontal meridian and the midsagittal plane at 14, 22, and 30 dB above their detection threshold.

METHODS

Subjects

Eleven subjects (4 females and 7 males) between 20 and 37 years old participated in this study with informed consent. All procedures conformed to the Declaration of Helsinki and were approved by the U.C. Davis Committee on Human Experimentation. Three subjects (D, E, and J) had extensive experience serving as subjects in sound localization tasks. Four subjects (B, G, H, and I) had participated in other sound localization tasks, but they had minimal previous experience in the paradigms used in this report. The remaining four subjects were naive to any sound localization paradigm, although two of them (A, F) had participated in other acoustic studies. All subjects had normal hearing, with threshold estimates within the normal range and varying about 12 dB across subjects.

Stimuli and apparatus

Experiments were conducted in a double-walled, sound-attenuated booth (IAC) with Sonex foam lining all the surfaces inside the booth. Stimuli were presented from 9 speakers (3.5-in. Pyle dual cone DD2) linearly aligned along either the horizontal meridian or the midsagittal plane at locations of 0 and ± 4°, 12°, 20°, and 28° relative to directly in front of each subject. Stimuli were 200-ms-duration (5-ms linear rise / fall) broadband (gaussian) noise. A personal computer and a Tucker–Davis Technologies (TDT; Gainesville, FL) digital signal processing system were used for stimulus presentation and data acquisition (see Recanzone et al. 1998).

Stimulus intensities presented in each experimental session were 14, 22, and 30 dB above detection threshold at each location. The highest intensity was chosen at 30 dB above threshold because pilot studies indicated that subjects were able to localize these noise stimuli at this intensity as well as they could at higher intensities in this localization paradigm. All subjects were able to detect the lowest intensity level (14 dB above threshold) on every trial. The most experienced subject (J) had the lowest spatial discrimination thresholds and was tested at 9, 17, and 25 dB above threshold. The data at 9, 17, and 25 dB above threshold detection for this subject were pooled with the data at 14, 22, and 30 dB above detection threshold from the other subjects.

Psychophysical tasks

Each experimental session was approximately 45 minutes and consisted of three segments in the following order: estimation of detection thresholds, brief training at the go / no-go paradigm, and measurement of sound localization performance. Azimuth and elevation sound localization performance and thresholds were defined in separate sessions. Each subject was seated in a chair with his / her head in an attached head brace to ensure that the distance between the center of the subject's interaural axes and the center of each speaker was 146 cm and that the head was oriented toward the center of the speaker array.

Detection thresholds

Auditory detection thresholds for all the locations used were estimated for each subject before each experimental session using a 1-up / 1-down adaptive tracking paradigm (Niemiec and Moody 1995). Subjects pressed a button to initiate a block of 30 consecutive stimulus presentations (interstimulus interval randomly varied between 1100 and 1800 ms) at each location. Subjects were instructed to keep the button depressed when they detected the auditory stimulus and to release the button when they did not. Auditory stimuli were presented simultaneously with a red LED (200-ms duration for both auditory and visual stimuli). The first stimulus was presented at 25–40 dB SPL depending on the initial assessment of the subject's detection threshold. If the button was depressed (detection), then the sound intensity of the subsequent stimulus was decreased by 5 dB. If the button was released (no detection), then the sound intensity of the subsequent stimulus was increased by 5 dB. Detection threshold for each location was estimated by averaging the intensity of the last six reversals (detection / no detection). These detection thresholds were used to define the stimulus intensities tested in each subject in the sound localization task (14, 22, and 30 dB above detection threshold).

Sound localization thresholds

The go / no-go paradigm used here has been described in detail previously (Recanzone et al. 1991, 1998). Briefly, subjects pressed a button to initiate a trial. S1 stimuli were presented two to five times from the center location (0° in azimuth and elevation), followed by one presentation of the S2 stimulus, which was presented from ± 4°, 12°, 20°, or 28° eccentricity along either the horizontal meridian or the midsagittal plane (Fig. 1). Subjects were instructed to release the button immediately after they detected a change in the stimulus location. Catch trials (S2 presented from the same location as S1) were also included in each session. Each session consisted of 15 randomly interleaved trials at each of the nine locations and each of the three intensities. The stimulus intensity was varied over a range of 3 dB in 1-dB steps to prevent subjects from using small differences of intensity between the speakers as cues for location changes.

Two training sessions (10–20 trials / session) were provided to allow all subjects to become comfortable with the task and to establish their criteria for what constituted a location change. The first training session consisted of only catch trials, the second session presented catch trials and S2 locations of ± 20° and ± 28° at the two highest intensities. Once the subjects reported that they understood the paradigm, the

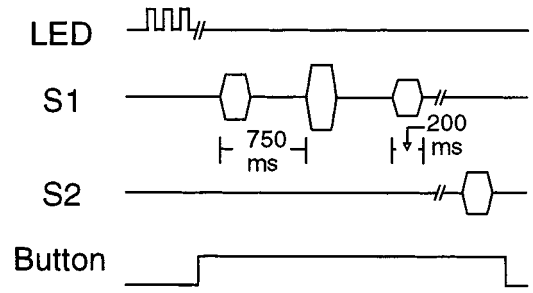

FIG. 1. Schematic of the behavioral paradigm. An LED flashed until the subject depressed the button and then it was extinguished. Broadband noise stimuli (200-ms duration) that varied in intensity over a 3-dB range were presented from directly in front of the subject every 750 ms. S1 (always the center location) was presented 2–5 times, followed by S2 presented from a different location. The subjects were instructed to release the button when they detected that the S2 was presented. S2 stimuli at each stimulus intensity were presented on randomly interleaved trials.

experimental session followed and was performed as described above. Subjects were not informed on the number of catch trials in the experimental session.

Data analysis

Psychometric functions were defined for each stimulus intensity in each subject following previous conventions (Recanzone et al. 1991, 1998). A button release within 750 ms of the S2 onset was recorded as a Hit (H), failure to respond was recorded as a Miss, and a response before the onset of the S2 was recorded as a False-Positive (FP). The FP rate (FPr) in each session was defined as (#FP / total # of trials). For the catch trials, a button release within 750 ms of the S2 onset was a False-Positive but it was recorded as a Hit in order to include a performance measure at the 0° location and create continuous psychometric functions. The Hit rate (Hr) was calculated by dividing the number of Hits by the sum of Hits and Misses recorded for each stimulus location and intensity. The performance (P) at each stimulus location and intensity was corrected by the FPr and computed as $P = \mathrm{Hr} \times (1 - \mathrm{FPr})$. For FPr below 15%, P is a reliable assessment of subjects' psychophysical performance and is strongly correlated with d' (see Recanzone et al. 1991, 1992, 1993, 1998). Statistical analyses were performed using the SPSS for Windows software (SPSS, Inc., Chicago, IL).

RESULTS

The false-positive rate (FPr) across all sessions and subjects was low, averaging 2.0% with a range of 0%–6.7%. The FPrs between sessions testing localization in azimuth and elevation were not statistically different from each other [paired, 2-tailed *t*-test; $t_{(10)} = 2.23$; $p > 0.05$]. The mean and standard deviation of the detection thresholds across speaker locations in both azimuth and elevation were calculated for each subject. Among the 11 subjects, the standard deviation of these detection thresholds ranged from 0.3 to 1.9 dB across locations in azimuth and from 0.9 to 2.6 dB across locations in elevation. Thus, the differences in the detection thresholds across locations were generally small. These detection thresholds averaged across subjects and locations were 8.0 ± 3.1 dB in azimuth and 7.1 ± 3.1 dB in elevation, which were not significantly different from each other [paired, 2-tailed *t*-test; $t_{(10)} = 0.99$; $p > 0.05$].

Psychometric functions

The ability to detect changes in stimulus location in azimuth and elevation was measured in 11 subjects at 3 stimulus intensities relative to their detection threshold. Representative examples from 2 subjects are shown in Figure 2. In both representative subjects, performance decreased with decreasing stimulus intensity. This is most evident at the lowest stimulus intensities, where the performance measured at 14 dB above detection threshold (solid triangles) was lower than the performance measured at 30 dB above detection threshold (solid diamonds) for almost all stimulus locations, particularly in elevation.

The results across subjects are summarized in Figure 3. There was no difference between localization performance to the left or right of midline at any stimulus intensity [Fig. 3, diamonds and solid line; paired, 2-tailed *t*-test at each eccentricity, $0.29 < t_{(10)} < 1.84$; $p > 0.05$]. This was also true for localization of stimuli presented above and below the horizontal meridian [Fig. 3, squares and dashed line; $0.03 < t_{(10)} < 2.19$; $p > 0.05$], with one exception at 22 dB above detection threshold in which the performance at 20° above the horizontal meridian was significantly worse than the performance at 20° below the horizontal meridian [$t_{(10)} = 3.09$; $p < 0.05$]. Since the performances in both directions in azimuth and elevation were symmetrical in all but one case, the performances at the same eccentricity in azimuth (left and right) and elevation

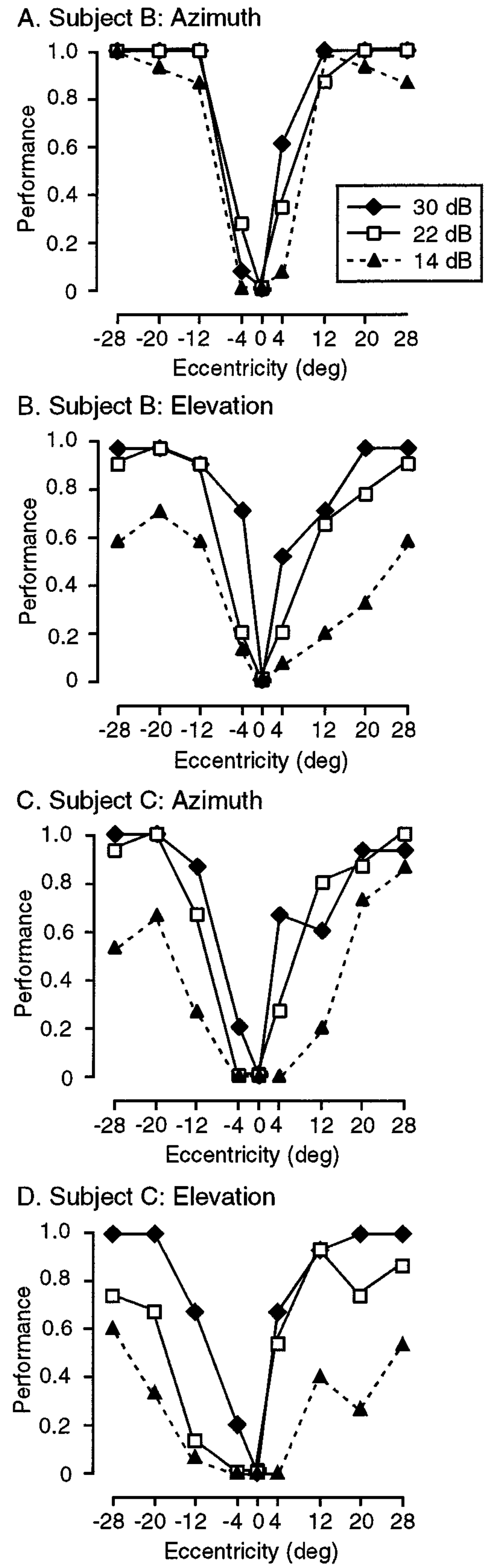

FIG. 2. Psychometric functions from two representative subjects. Each panel shows the performance (*y* axis) as a function of the S2 stimulus eccentricity (*x* axis) at three different intensity levels (see inset). Results from subject B are shown for azimuth (**A**) and elevation (**B**) and results from subject C are shown for azimuth (**C**) and elevation (**D**). In each case the localization performance was degraded at the lowest stimulus intensity and the degradation was larger in elevation than in azimuth. Positive eccentricities correspond to rightward and upward locations in azimuth and elevation, respectively.

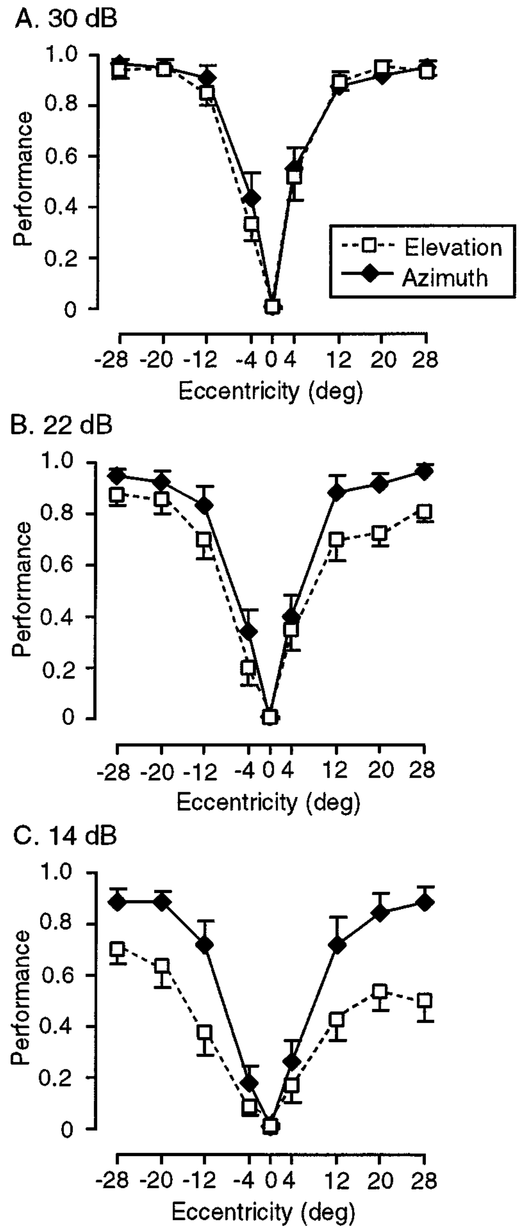

FIG. 3. Mean psychometric functions across subjects. Each symbol shows the mean performance across subjects. Error bars indicate the standard errors of the mean (SEMs) and are shown in only one direction for clarity. **A**. Mean psychometric functions in azimuth (—♦—) and elevation (- -□- -) at 30 dB above detection threshold. **B**. 22 dB above detection threshold. **C**. 14 dB above detection threshold. In both azimuth and elevation, localization ability worsened as the intensity was decreased. There was no difference between elevation and azimuth localization ability at 30 dB, but localization in elevation was significantly worse than that in azimuth at 22 and 14 dB above detection threshold.

(up and down) were considered equivalent and combined for further analysis.

A 3 (intensity) × 4 (eccentricity) factorial repeated-measures ANOVA analyzed separately for elevation and azimuth showed that the subjects' performance significantly improved with increasing eccentricity, as evident in Figure 3 [elevation: $F_{(3,30)} = 71.20$, $p < 0.001$; azimuth: $F_{(3,30)} = 69.06$, $p < 0.001$]. A main effect of intensity on performance was also observed in both elevation and azimuth [elevation:$F_{(2,20)} = 85.37$, $p < 0.001$; azimuth: $F_{(2,20)} = 22.97$, $p < 0.001$]. The difference between the elevation and azimuth repeated-measures ANOVAs was that there was an interaction effect between intensity and eccentricity for localization in azimuth [$F_{(6,60)} = 4.76$, $p < 0.001$] but not in elevation [$F_{(6,60)} = 2.19$, $p > 0.05$]. Further analysis on intensity (level-to-level contrast) showed that each decrease of 8 dB significantly degraded subjects' performance in elevation [30–22 dB above threshold: $F_{(1,10)} = 78.409$, $p < 0.01$; 22–14 dB above detection threshold: $F_{(1,10)} = 59.980$, $p < 0.01$]. The lack of an interaction effect between intensity and eccentricity for elevation indicates that this significant level-to-level effect of intensity occurred at each eccentricity, extending to as far as 28°.

For azimuth, a significant interaction effect between the intensity and eccentricity indicated that the effect of intensity on the subjects' performance was not similar across the eccentricities tested. Level-to-level contrasts of the intensity factor at each eccentricity showed that, at 12°, 20°, and 28°, subjects did equally well at 30 and 22 dB above detection threshold [Figs. 3A, B, diamonds and solid line; $F_{(1,10)} = 2.79$, 1.23, and 0.0 for 12°, 20°, and 28°, respectively, all $p > 0.05$], but their performance became significantly worse when the intensity was decreased from 22 to 14 dB above detection threshold [Figs. 3B, C, $F_{(1,10)} = 7.18$, 5.12, and 5.36 for 12°, 20°, and 28°, respectively, all $p < 0.05$). At 4° in azimuth, each 8-dB decrease resulted in a significant decrease in subjects' performance (30 to 22 dB above detection threshold: $F_{(1,10)} = 8.19$, $p < 0.05$; 22 to 14 dB above detection threshold: $F_{(1,10)} = 13.91$, $p < 0.01$].

Although an intensity effect on localization ability was found in both azimuth and elevation, across subjects the degradation in performance was greater for localization in elevation than for localization in azimuth (Fig. 3; note that the distance between the azimuth and elevation psychometric functions increases from panel B to C). At 30 dB above detection threshold, the localization performances in azimuth and elevation were not significantly different from each other at any eccentricity tested [Fig. 3A; paired, 2-tailed *t*-test at each corresponding eccentricity; $0.40 < t_{(10)} < 1.74$; $p > 0.05$]. At both 22 and 14 dB above detection threshold, localization performance in azimuth was significantly better than that in elevation at all eccentricities [paired, 2-tailed *t*-test at each eccentricity; $3.53 < t_{(10)} < 6.81$; $p < 0.01$], except at 4° [22 dB above detection threshold: $t_{(10)} = 1.80$, $p > 0.05$; 14 dB above detection threshold: $t_{(10)} = 1.171$, $p > 0.05$]. Although Figures 3B, and C showed that performance at 4° of eccentricity in azimuth was better than that in elevation at the two lowest intensities (Figs. 3B, C), the difference in performance at this eccentricity between localization in azimuth and elevation was not statistically different since both were below the sound localization performance of 0.5 and their variances were large. Therefore, in this paradigm, the ability to discriminate a change in sound location of 4° at the two lowest intensities tested was difficult in both azimuth and elevation, with localization performance in elevation more impaired than localization in azimuth for eccentricities greater than 4° at the two lower intensities.

Intensity effects on localization thresholds

The preceding analysis indicates that sound localization performance is degraded in both azimuth and elevation at low stimulus intensities across a broad spatial range. In order to directly compare the sound localization acuity between azimuth and elevation as a function of stimulus intensity, sound localization thresholds were calculated in all subjects. Sound localization thresholds in azimuth and elevation were defined in both directions (up and down; left and right) at each intensity tested as the eccentricity at which the subject's performance was 0.5 (linearly interpolated from the two data points bracketing the 0.5 performance level), following previous conventions (Recanzone et al. 1991). A 2 (direction) × 3 (intensity) factorial repeated-measures ANOVA on thresholds in azimuth and elevation (analyzed separately) indicated that there was no effect of direction [left vs. right in azimuth: $F_{(1,8)} = 2.04$, $p > 0.05$; up vs. down in elevation: $F_{(1,8)} = 0.03$, $p > 0.05$] at any intensity level [interaction effect in azimuth: $F_{(2,16)} = 0.71$, $p > 0.05$; in elevation: $F_{(2,16)} = 0.38$, $p > 0.05$]. Thus, the thresholds for both directions (up compared with down; right compared with left) were considered to be equivalent at each intensity level tested, and the following analysis was conducted on the average of the two values.

Figure 4 shows the sound localization thresholds at 30, 22, and 14 dB above detection threshold for all subjects in azimuth (Fig. 4A) and elevation (Fig. 4B). Bars labeled with ">28" in Figures 4A and B indicate that the localization threshold could not be measured because the performance at 28° of eccentricity in at least one direction was less than 0.5 (subjects J and K). Although the range of localization thresholds in elevation at the lower intensities across subjects was large (e.g., 4.5° to >28° at 14 dB; Fig. 4B), each subject showed a consistent pattern of increasing sound localization thresholds in both elevation and azimuth as a function of decreasing intensity, with larger sound localization thresholds in elevation than in azimuth at the two lowest intensities (Figs. 4A, B).

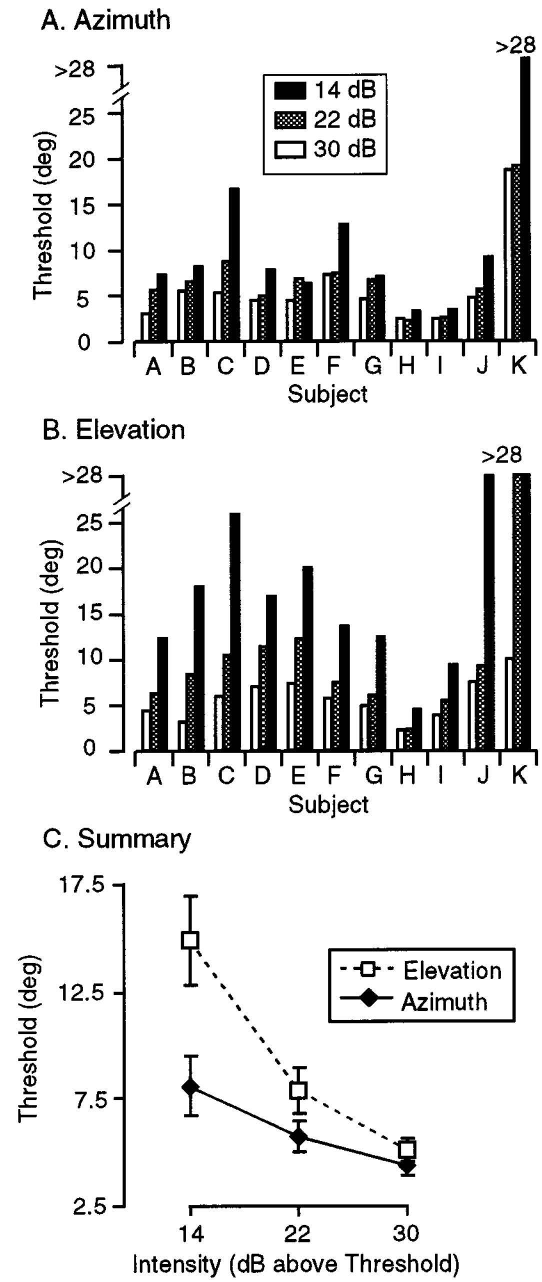

FIG. 4. Sound localization thresholds for each subject. Each set of bars shows the threshold measured in azimuth (**A**) and elevation (**B**) in the 11 subjects tested. Solid bars: 14 dB, shaded bars: 22 dB, open bars; 30 dB above detection threshold. **C**. Mean thresholds across subjects in azimuth (—♦—) and elevation (--□--). Error bars show the SEMs. Note that sound localization thresholds decreased with increasing intensity.

These observations were qualified statistically by pooling the data from the nine subjects in which the sound localization thresholds could be measured (data from subjects J and K were not included). The pooled localization thresholds in azimuth and elevation as a function of stimulus intensity are shown in Figure 4C. There was a main effect of intensity on the localization thresholds in elevation [Fig 4C; repeated-measure ANOVA; $F_{(2,16)} = 29.64$, $p < 0.01$]. Level-to-level contrast analysis of intensity showed that the localization thresholds increased significantly with each decrease of 8 dB in intensity [30 to 22 dB above detection threshold: $F_{(1,8)} = 19.08$, $p < 0.01$; 22 to 14 dB above detection threshold: $F_{(1,8)} = 30.58$, $p < 0.01$]. The analysis for localization thresholds in azimuth revealed similar results: There was a significant main effect of intensity on localization thresholds [repeated-measure ANOVA; $F_{(2,16)} = 9.87$, $p < 0.01$], and the thresholds became significantly larger when the intensity was decreased by 8 dB [30 to 22 dB above detection threshold: $F_{(1,8)} = 8.95$, $p < 0.05$; 22 to 14 dB above detection threshold: $F_{(1,8)} = 7.24$, $p < 0.05$]. Thus, each decrease in intensity of 8 dB across the studied range significantly degraded the subjects' localization performance in both elevation and azimuth.

A 2 (dimension: azimuth or elevation) × 3 (intensity) factorial repeated-measures ANOVA revealed that the localization thresholds in elevation were significantly larger than those in azimuth [$F_{(1,8)} = 15.42$, $p < 0.01$]. There was also a significant interaction effect between dimension and intensity [$F_{(2,16)} = 21.44$, $p < 0.01$], indicating that the effect of intensity on sound localization performance was different between azimuth and elevation. At 30 dB above detection threshold, there was no difference between the localization thresholds for azimuth and elevation [paired, 2-tailed *t*-test; $t_{(8)} = 1.43$, $p > 0.05$], demonstrating that the subjects were able to localize equally well in azimuth and elevation at this intensity. At 22 and 14 dB above detection threshold, the sound localization thresholds in elevation were significantly larger than those in azimuth [paired, 2-tailed *t*-test; 22 dB above detection threshold: $t_{(8)} = 6.95$, $p < 0.05$; 14 dB above detection threshold: $t_{(8)} = 23.59$, $p < 0.01$]. Therefore, the same 8-dB decrease in the intensity from 30 to 22 dB degraded the subject's ability to localize sounds in elevation to a greater extent than in azimuth. This also occurred in the subsequent 8-dB decrease from 22 to 14 dB above detection threshold. These results indicate that the effect of stimulus intensity on localization was greater in elevation than in azimuth.

To further investigate the interaction effect of intensity between localization in azimuth and elevation, the differences in sound localization thresholds between adjacent intensity levels tested in azimuth and elevation were measured in each subject and pooled together for statistical comparison (Fig. 5). Although the sound localization threshold at 30 dB above detection threshold was equivalent in azimuth and elevation (Fig. 4C), the localization thresholds in elevation increased at a faster rate compared with that in azimuth as a function of decreasing stimulus intensity. For localization in elevation, the increase in the localization threshold from 22 to 14 dB above detection threshold was significantly larger than that from 30 to 22 dB [right bars of Fig 5; 7.0° ± 1.3° vs. 2.8° ± 0.6°; paired, 2-tailed *t*-test; $t_{(8)} = 4.49$, $p < 0.01$]. However, the localization threshold increases in azimuth from 22 to 14 dB and from 30 to 22 dB above detection threshold were not significantly different from each other [left bars of Fig. 5; 2.4° ± 0.9° vs. 1.3° ± 0.4°; paired, 2-tailed *t*-test; $t_{(8)} = 1.18$, $p > 0.05$]. Therefore, the change in localization performance can be considered to be relatively constant for azimuth over this intensity range, whereas the change in performance for elevation decreased at a more rapid rate as the stimulus intensity neared detection threshold.

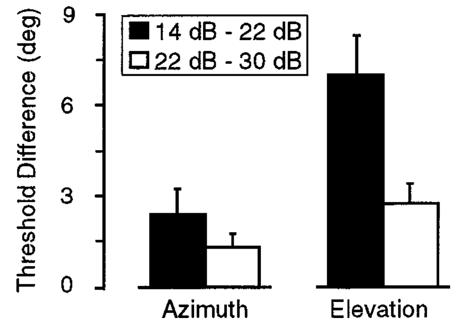

FIG. 5. Differences in the sound localization thresholds between intensity levels. Solid bars show differences in thresholds between 14 and 22 dB above detection threshold; open bars show differences in thresholds between 22 and 30 dB above detection threshold. Error bars represent the SEMs. The threshold differences across the indicated intensity levels (solid vs. open bars) were not statistically different in azimuth but they were significantly different in elevation. The threshold differences in elevation were significantly larger than the corresponding ones in azimuth.

We also considered the possibility that the task difficulty may change within a session depending on the number of S1 stimuli that were presented. A 4 (eccentricity) × 4 (number of S1) repeated-measures ANOVA showed a significant effect of the number of S1 stimuli in both the azimuth and the elevation conditions. A level-to-level contrast analysis showed that the performance on trials with two S1 stimuli was significantly worse than trials with three or more S1 stimuli, but the performances on trials with three, four, and five S1 stimuli were not significantly different from each other. This suggests that the discrimination performance remained constant when there were greater than two S1 stimuli. However, there was no significant interaction effect between eccentricity and S1, indicating that a significantly worse performance on trials with only two S1 stimuli was consistently observed across all the eccentricities tested. As a result, our localization thresholds could be systematically inflated but should not change the main finding that there was a differential effect of stimulus intensity on sound localization ability in elevation and azimuth. To verify this assertion, the same statistical analyses as described above were conducted using only trials in which there were at least three S1 stimuli presented. As expected, thresholds were slightly lower but there was no difference in the statistical significance of any comparisons described above between the analysis when all trials were used versus when restricted to only trials when three or more S1 stimuli were presented.

DISCUSSION

The present study describes a degradation in sound localization ability in both azimuth and elevation at stimulus intensities near detection threshold in the same subjects. There are three main findings in this study: (1) localization is degraded at low stimulus intensities, (2) localization in elevation is worse than that in azimuth at intensities near detection threshold, and (3) the degradation in localization occurs more rapidly in elevation than in azimuth as the stimulus intensity decreases toward detection threshold.

Experimental paradigm

One concern regarding the go / no-go paradigm used in this study is that direct comparisons to previous studies using a two-alternative forced-choice procedure are difficult (e.g., Perrott and Saberi 1990; Perrott et al. 1993). We initially used a two-alternative forced-choice procedure for the localization in elevation but found that the naive subjects had great difficulty in establishing reliable criteria with which to perform the task. Increasing the number of S1 stimuli seemed to aid the naive subjects in making this discrimination, based on reports by the subjects that used both methods. The go / no-go paradigm is well suited for the objectives of this study for several reasons: (1) subjects are forced to make rapid decisions (within 750 ms), (2) in the absence of feedback, subjects typically do not adjust their criteria during the session, and (3) the go / no-go paradigm can also be used for studies in experimental animals. Monkeys can be easily trained at a variety of auditory discrimination tasks using this paradigm (e.g., Brown et al. 1978, 1980, 1982; Recanzone et al. 1993, 2000; Sinnott et al. 1987; Sinnott and Kreiter 1991). Therefore, the results of this study can be used to directly compare the performance of humans subjects to data collected in future studies on monkeys.

A second concern regarding the present paradigm is that subjects may be using speaker-specific or other nonspatial cues to determine the location changes. In-depth controls completed in our previous study that used the same experimental setup and behavioral paradigm showed that the subjects relied mainly on spatial cues when performing this task (Recanzone et al. 1998). The likelihood that subjects used nonspatial cues in order to perform this task is low, considering that we had used training sessions, roved the intensity across a 3-dB range between stimulus presentations, and found different performance in azimuth compared with that in elevation although the same speakers were used in both tasks. After completing the sessions, subjects also reported that they had used spatial cues to perform the task.

A final concern is regarding the way detection thresholds were determined in the present study. We measured the sound localization performance at three stimulus intensities based on our estimates of detection threshold using an adaptive tracking paradigm. Since the subjects were informed that there would be stimuli that they could not detect, this paradigm was effective in obtaining reliable thresholds, as indicated by the similarity between the thresholds measured for each different speaker within a session. However, we found in pilot studies that naive subjects had great difficulty in performing this psychophysical task without some indication of when a stimulus could occur. We addressed this by pairing a visual stimulus to the presentation of the auditory stimulus, which may have caused a response bias resulting in an underestimation of their detection threshold. However, the results of this study are not dependent on the actual values of each stimulus intensity, as each subject localized stimuli at the three intensities on randomly interleaved trials. Also, the main focus of the study was to compare sound localization ability at stimulus intensities decreasing toward detection threshold. Changes in the stimulus intensities of only a few dB (due to a small and systematic error in estimating thresholds across speakers) would not influence the main findings that sound localization performance degrades at stimulus intensities near threshold and that this degradation is greater for localization in elevation than for localization in azimuth.

Comparisons to previous studies

Previous studies that investigated the effect of intensity on sound localization have shown that localization ability deteriorates along the horizontal meridian at low intensities (e.g., <30 dB, Altshuler and Comalli 1975; Comalli and Altshuler 1976; Recanzone et al. 1998), and this study extends those findings to show that this intensity effect also occurs for localization along the midsagittal plane. The localization thresholds measured in this study for horizontal and vertical localization at 30 dB above detection threshold are similar to those described in macaque monkeys (Recanzone et al. 2000) also using a go/no-go paradigm. The degradation in localization ability in azimuth and elevation with decreasing stimulus intensity is also consistent with recent observations in macaque monkeys (Su et al. 2000).

Compared with a previous study (Recanzone et al. 1998) that used the same duration noise stimuli, paradigm, and experimental equipment, the discrimination thresholds found in the present study are slightly higher than those found in that study. Several reasons may account for these differences. First, the percentage of the present study subjects extensively trained in the psychophysical paradigm was smaller (3 of 11 subjects) than that in the previous study (3 of 5 subjects). The higher number of naive subjects may account for the average performance being worse in this study. Second, the majority of subjects in this study participated in only one session for localization in azimuth and another session for localization in elevation. Only three subjects performed more than one experimental session (but not more than four, including pilot sessions) for either horizontal or vertical localization (subjects D, F, and G). In contrast, the five subjects reported in Recanzone et al. (1998) performed multiple sessions that may have contributed to the better performance reported in that study. Third, sessions in the current study consisted of randomly interleaved trials of different stimulus intensities. The increased difficulty of the task at the very low intensities could have resulted in a more conservative criteria for making a response. This is supported by the finding that the false-positive rates for the current study (maximum 6.7%) were smaller than those reported previously (maximum 8%; Recanzone et al. 1998).

Sound localization thresholds in azimuth measured at the highest intensity in the present study are in general agreement with, although slightly higher than, those reported in previous studies that used different paradigms (e.g., Roffler and Butler 1967; Chandler and Grantham 1992). One reason that may account for this difference in threshold measurements is that the difficulty of the trials presenting low stimulus intensities in this study may have caused the subjects to establish a more conservative response criteria. This is supported by the low false-positive rates found across subjects, as discussed earlier. Secondly, subjects performed significantly worse when only two S1 stimuli were presented compared with trials where three or more S1 stimuli were presented, suggesting that subjects were less ready to make a response when fewer than three S1 stimuli were presented. Although this difference in performance was consistent across intensities and eccentricities, it would serve to increase localization thresholds when all trials were pooled together. However, similar analysis restricted to only the trials with three or more S1 presentations showed no difference in the main results of this study, namely, that localization ability deteriorated significantly at lower stimulus intensities in both azimuth and elevation and that localization in elevation was more deteriorated than localization in azimuth.

Another potential reason that larger localization thresholds were found in this study is that the spatial resolution used to measure performance may not have been fine enough to accurately define thresholds at the highest intensity condition. This may also be why there was no difference between azimuth and elevation thresholds at the highest intensity in our task, while others found small differences (1°–3°) for localization in azimuth and elevation in the frontal space (e.g., Makous and Middlebrooks 1990; Carlile et al. 1997). However, we chose these identical separations for localization in both azimuth and elevation at each of the three stimulus intensities in order to directly compare the performance between these two dimensions across stimulus intensities and eccentricities (see "Psychometric Functions" in Results). This potential overestimation of the azimuth localization thresholds at the highest intensity condition would not change our main findings; for example, the filled diamond plotted at 30 dB above threshold in Figure 4C would be shifted downward, indicating that the intensity effect on azimuth localization would have been even larger.

Effects of intensity on sound localization ability

The results of this study show that decreasing the intensity toward detection threshold degrades localization ability in both azimuth and elevation. The degradation in sound localization performance near detection threshold can be interpreted to reflect an inability of the subjects to detect frequency components in the acoustic signal that provide important localization cues. This inability to detect some cues reflects the ability of the nervous system to encode acoustic space. Auditory cortical lesions result in sound localization deficits (Jenkins and Merzenich 1984; Kavanaugh and Kelly 1987; Heffner and Heffner 1990), and several studies have attempted to understand how cortical neurons could represent the spatial attributes of acoustic stimuli (e.g., Eisenman 1974; Benson et al. 1981; Middlebrooks and Pettigrew 1981; Brugge et al. 1996; Middlebrooks et al. 1998; Recanzone et al. 2000). Recent evidence from macaque monkeys indicates that while most individual neurons in the primate auditory cortex do not have the spatial resolution necessary to account for sound localization acuity, pooling the responses of these broad, spatially tuned cortical neurons does provide sufficient information to account for sound localization ability at stimulus intensities of approximately 65 dB SPL (Recanzone et al. 2000).

One way to reduce localization ability is to decrease the bandwidth of the stimulus. Broadband stimuli contain more localization cues than narrowband and tone stimuli, thereby resulting in more populations of spatially sensitive neurons activated to encode acoustic space across frequencies. For example, for high-intensity broadband stimuli, responses from neurons sensitive to the spatial location of low, mid, and high frequencies could all contribute to the computation of acoustic space. In contrast, narrowband or tone stimuli would activate only populations of neurons that respond to those stimulus frequencies, thereby reducing the ability to compute the spatial location of the stimulus. In elevation, the identification of the frequency of spectral notches created by the HRTF, which vary over a restricted range in the region of frontal space (Carlile and Pralong 1994), is thought to be a very potent cue for localization along this dimension. Thus, the populations of neurons that could potentially encode elevation information would be concentrated to those responding to high frequencies.

A second way to decrease the available cues, both binaural and spectral, is to decrease the stimulus intensity. The average human audiogram for broadband stimuli indicates that the thresholds of many frequency components are either near or below the lowest intensity level used in the present study (Glasberg and Moore 1990). Decreases in the intensity of a broadband stimulus would primarily affect the detection of the lowest and highest audible frequencies (which have the highest thresholds), thereby decreasing the available binaural cues. As stimulus intensity decreases, decreases in energy at the frequencies corresponding to the spectral notches would similarly make these frequencies inaudible and, thus, make the identification of the notch frequencies ambiguous.

By decreasing the stimulus intensity of broadband noise, the ability of the nervous system to process elevation cues, particularly the notches, would be affected to a greater extent compared with the ability to process the binaural cues used for localization in azimuth. This is indicated by the behavioral results obtained in the present study that revealed that stimulus intensity had a larger effect on localization performance in elevation where the subjects' ability to localize sounds in elevation was significantly more impaired than in azimuth at the two lowest intensity levels (14 and 22 dB above detection threshold). Furthermore, across the intensity range tested (from 14 to 30 dB above threshold), the degradation rate of the localization ability in elevation was larger than that in azimuth (Fig. 5). As the intensity decreased, the degradation in performance occurred across eccentricities up to 28° in elevation, but not in azimuth (Fig. 3). Most subjects, however, could still localize some of the stimuli in elevation, even at the lowest intensity (e.g., Fig. 3C, compare performance at 28° to those at smaller eccentricities). This suggests that not all the spectral notch information in the HRTFs was missing at the lowest intensity levels tested and/or that non-notch spectral cues serve an important role in localization at intensities near detection threshold.

Currently there are no available data concerning how populations of primate auditory cortical neurons are activated with increasing stimulus intensity. Studies in the cat indicate that there is a non-linear increase in the percentage of neurons activated with increasing stimulus intensity near detection threshold (Phillips et al. 1994). As the stimulus intensity increases from detection threshold, more localization cues are audible to the listener and more populations of spatially sensitive neurons responding to different frequency ranges can contribute to the processing of acoustic space. At higher stimulus intensities, the increase in the sizes of these populations of spatially sensitive neurons increases more slowly and can stabilize because of the neurons with non-monotonic rate/level functions. This stabilization may explain why sound localization performance is relatively constant across stimulus intensities well above threshold (Altshuler and Comalli 1975; Comalli and Altshuler 1976; Recanzone et al. 1998). At higher stimulus intensities, sound localization ability is not expected to improve because the information encoded across the populations of neurons that participate in spatial computation will likely saturate once a critical size has been reached (see Sahdlen and Newsome 1998; Furukawa and Middlebrooks 2000).

The results of the present study indicate that stimulus intensity may provide a useful tool in experiments designed to test correlations between the neurophysiological and behavioral basis of sound localization. As sound localization behavior can be significantly affected as a function of stimulus intensity, the ability of central neurons that encode spatial information should similarly be degraded at low stimulus intensities. Taking advantage of the finding that there is a degradation in sound localization performance at low stimulus intensities in an animal model may provide a valuable tool in elucidating the neuronal mechanisms of sound location perception.

SUMMARY

This study revealed that the ability to localize sounds in both azimuth and elevation was degraded at stimulus intensities near threshold in normal human subjects. The degradation in performance was greater for localization in elevation than in azimuth, and the rate of degradation increased near detection threshold in elevation but not in azimuth.

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