Comparison of relative and absolute sound localization ability in humans

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(Received 25 March 1997; accepted for publication 28 October 1997)

Sound localization ability has traditionally been studied using either a relative localization task, where thresholds to determine a difference in sound source location is approximately 1–10 degrees, or an absolute localization task, where the range of estimates of the source of a sound are 4–30 degrees. In order to directly relate these two psychophysical methods, we compared the psychometric functions from a relative localization task in a human subject to the same subject's performance on an absolute localization task using three different acoustic stimuli: Gaussian noise, 1-kHz tones, and 4-kHz tones. The results showed that the relative localization threshold was a poor indicator of the range of estimates of the same stimulus in absolute space, however, the width of the relative localization psychometric functions was well correlated with the width of the distribution of estimates made in the absolute localization task. It is concluded that the relative localization psychometric functions, but not threshold, provides a reliable estimate of absolute spatial localization ability in human subjects, and suggested that the same neuronal mechanisms can underlie the psychophysical data using both methods. © *1998 Acoustical Society of America.* [S0001-4966(98)03002-1]

PACS numbers: 43.66.Qp, 43.66.Ba, 43.64.Bt [JWH]

INTRODUCTION

The ability of humans and animals to localize acoustic stimuli is generally tested using one of two psychophysical procedures: relative localization thresholds measure the ability to determine that a repeated stimulus has changed location (e.g., Mills, 1958; Molino, 1974; Perrott, 1984; Terhune, 1985; Perrott and Saberi, 1990; Chandler and Grantham, 1992; Perrott *et al.*, 1993; see Middlebrooks and Green, 1991), and absolute localization thresholds measure the ability to determine the location in space of a single stimulus (e.g., Stevens and Newman, 1936; Newton, 1983; Oldfield and Parker, 1984; Butler, 1986; Perrott *et al.*, 1987; Wightman and Kistler, 1989; Makous and Middlebrooks, 1990; Middlebrooks, 1992; Ahissar *et al.*, 1992; Butler and Musicant, 1993; Wenzel *et al.*, 1993; Good and Gilkey, 1996). These studies indicate that most individuals have relative localization thresholds of a few degrees, whereas the absolute localization of sounds is broader, depending on the eccentricity and spectral content of the stimulus.

The difference between these two measures is yet to be resolved, and it has been suggested that the relative localization paradigm originally described (Mills, 1958) was actually a reflection of an absolute discrimination task (Hartmann, 1989). However, to date it is difficult to directly compare the results of the two types of studies from the literature due to the differences of the paradigms and subjects, as well as differences in the spectral content, amplitude, and duration of the acoustic stimuli.

Resolution of this issue is important for relating the sound localization ability to underlying neuronal mechanisms. The growing interest in the cortical and thalamic mechanisms of sound localization (e.g., Imig *et al.*, 1990; Rajan *et al.*, 1990; Middlebrooks *et al.*, 1994; Clarey *et al.*, 1995; Brugge *et al.*, 1996; Barone *et al.*, 1996) and the growing interest in the function of the cortical processing of acoustic information of the primate in general (e.g., Wang *et al.*, 1995; deCharms and Merzenich, 1996; Stricanne *et al.*, 1996; Rauschecker *et al.*, 1997) underscore the importance in understanding how these two measures of sound localization are related. It is likely that the two measures are dependent on the same auditory cortical structures, given the equivalent deficits revealed using both methods following auditory cortical ablations (Neff *et al.*, 1956; Heffner and Masterton, 1975; Heffner, 1978; Kavanagh and Kelly, 1987; Jenkins and Merzenich, 1984; Heffner and Heffner, 1990). It has been demonstrated that the spatial selectivity of auditory cortical neurons recorded in animals are much broader than the relative localization thresholds (Eisenman, 1974; Benson *et al.*, 1981; Middlebrooks and Pettigrew, 1981; Imig *et al.*, 1990; Rajan *et al.*, 1990; Middlebrooks *et al.*, 1994; Clarey *et al.*, 1995; Brugge *et al.*, 1996; Barone *et al.*, 1996), making it difficult to relate these measures of single cortical neurons to perceptual thresholds. Although the relative localization paradigms provide one estimate of localization ability, it may not be appropriate to compare relative localization thresholds to the receptive field sizes of cortical neurons. It may be more appropriate to compare the distribution of absolute localization estimates to the responses of cortical neurons. Alternatively, relative localization paradigms may accurately reflect neuronal processes, but some measure other than threshold could be directly related to single neuron activity. In either case, there should be a clear relationship

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between relative and absolute localization measures, given deficits in both tasks following cortical lesions.

In order to determine the relationship between these two localization paradigms, we used the same acoustic stimuli, apparatus, and human subjects to compare the psychometric functions from a relative localization task to the estimates of the sound source location from an absolute localization task. These subjects had relative and absolute localization performance similar to that seen from previous studies (cited above). Comparison between the two paradigms showed that the widths of the psychometric functions derived from the relative localization task were strongly correlated with the width of the range of the estimates recorded in the absolute localization task. These results indicate that the difference between the perceived locations in space of acoustic stimuli are in fact within the range of the spatial selectivity of a subset of cortical neurons, and that the width of the relative localization psychometric functions, but not the threshold, provides a good estimate of sound localization ability.

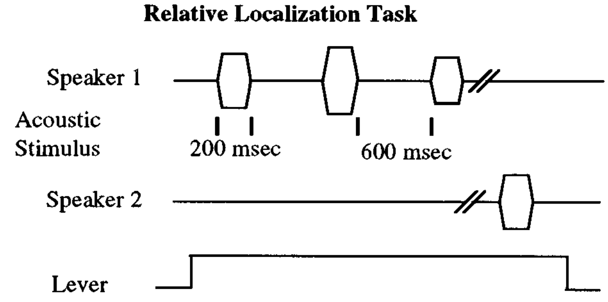

FIG. 1. Schematic of the timing of events during the relative localization task. Subjects initiated a trial by a lever press. A series of 200-ms duration sounds were presented with a 600-ms interstimulus interval. Subjects released the lever when they detected that the speaker changed location. Each acoustic stimulus varied in intensity over a 4-dB range.

I. EXPERIMENT I: RELATIVE LOCALIZATION MEASURES

A. Methods

1. Subjects

Three male (CK, WG, PS) and two female (AS and CC) subjects between 20–35 years of age at the time of testing performed these tasks with informed consent. Subjects had no known audiological deficits, and detection thresholds for the stimuli used were within normal limits (described below). All subjects had normal or corrected to normal vision. Three of the subjects had extensive psychophysical experience (CK, AS, and PS), and this was the first psychophysical acoustical study for the other two subjects (WG and CC). Subjects CK, WG, and CC completed a full series for each acoustic stimulus, while subject AS completed a full series of the absolute localization paradigm but only a partial series for the relative localization paradigm. Subject PS completed only the control experiments described below, and had partial results from the other two paradigms. The incomplete results from these two subjects were consistent with the findings from the subjects that completed each paradigm and will not be illustrated here.

2. Stimulus parameters

Stimuli were generated using a Tucker-Davis Technologies digital signal processing system. An i486 computer controlled all aspects of the psychophysical task, stimulus generation and delivery, and data collection. Three different stimuli were used: Gaussian noise, 1-kHz tones, and 4-kHz tones. All stimuli were 200 ms in duration with a 5-ms linear rise/fall. Stimuli were delivered through 1 of 15 different speakers ($3\frac{1}{2}$-in. Pyle dual cone DD2) located on an arc at a constant distance of 146 cm along the plane of the interaural axis, spanning a range of either -8 to 48 degrees (subjects CK, CC, WG, and PS) or 0 to 56 degrees (AS) in 4-degree increments. The entire behavioral apparatus was located within a double-walled acoustic chamber (6.5-$\times$8.5-ft inner dimensions; IAC) with 3-in. sound attenuating foam (Sonex) on all four walls, the ceiling, and much of the floor surrounding the subject.

Physical characteristics: Acoustic stimuli were measured using a B&K sound pressure meter with the microphone placed in the sound booth at the location occupied by the center of each subject's head, with all parts of the apparatus in place. The fast Fourier transform was calculated for all acoustic stimuli from each speaker location in the absence of the subjects. Speaker transformation functions showed a flat portion (± 3 dB) from 200 Hz to 12 kHz with approximately 6-dB/octave rolloff. Comparisons across speakers showed minimal differences in the magnitudes and phases of the FFT components for all three stimuli. Energy of the harmonic components of the tonal stimuli were <10 dB SPL; echo contributions to all stimuli were <20 dB SPL.

Psychophysical calibration: The detection threshold for each of the stimuli, at each of the speaker locations used for a given stimulus, were derived using a staircase method for each individual subject during several different periods throughout the study. All subjects had detection thresholds which were consistent with the normal human audiogram. Stimuli were sequentially presented across the speaker array at 30 dB above this threshold and the subjects were asked to adjust the overall intensity of each speaker until they were all the same intensity, which usually resulted in a change of less than 1 dB. These intensity values were randomly varied (± 2 dB) during the course of each trial for each subject. This perceptual equalization ensured that the subjects could not base their localization estimates on absolute loudness, and could only use interaural difference and the spectral cues due to the head-related transfer functions to localize these stimuli.

3. Psychophysical task

All psychophysical tasks were approved by the UC Davis Human Subjects Review Committee and abided by the ethical principles of psychologists. This psychophysical task was based on a go/no-go paradigm described in detail previously (Recanzone *et al.*, 1991; Fig. 1). Subjects were seated in a chair near the center of the sound booth with their heads held stationary by a modified headband attached to the ceiling of the sound booth. All experiments were conducted in sufficient darkness to prevent visualization of the apparatus, and no subject reported the ability to see the apparatus, even after sufficient time for dark adaptation to occur (>1 h).

Subjects initiated a trial by pressing a lever. A series of acoustic stimuli were presented from a single speaker (S1 stimulus) with a 600-ms pause between stimuli. After a randomly determined number of S1 stimulus presentations (2–6), the same acoustic stimulus was then presented from a different speaker location (S2). The subject was required to release the lever when they detected a change in the stimulus location. Additional ''catch'' trials were presented where stimuli were only presented from the S1 location. For tonal stimuli, seven different S2 speaker locations were used, separated by 8 degrees. Similarly, 15 different speaker locations were used for noise stimuli with the speaker locations separated by 4 degrees. In a given session, 15 trials for each of the S2 locations were presented from 7 of the possible 15 locations for the noise stimuli (separated by 4 degrees), and for 7 locations of 1 of the 2 tonal stimuli (separated by 8 degrees) as well as 15 catch trials for each stimulus for a total of 240 trials. The S2 speaker location and the type of sound stimulus (tone or noise) was randomly interleaved across trials. In three subjects, at least one session was conducted with the S1 stimulus at each of the 8 (tone) or 15 (noise) different S1 locations (16 sessions minimum for these subjects). Subjects AS and PS were not tested at all S1 locations for all stimuli.

Control experiments: Two different classes of control experiments were performed on three subjects (CC, CK, and PS) to ensure that subjects were using spatial cues to perform the task and not nonspatial cues such as differences in the speaker transformation functions. For tonal stimuli, single sessions were run using the same paradigm except that three different S1 locations were used on randomly interleaved trials (0, 24, and 48 degrees). One session each was run (15 trials/location, including catch trials) for 1- and 4-kHz tone stimuli. Each subject then performed a second set of sessions in which the speakers between pairs of locations were exchanged (8 with 16 degrees and 32 with 40 degrees).

The second class of control experiment tested each adjacent pair of speakers using noise stimuli. Subjects oriented their head and body to the location such that one speaker was on either side of the midline. Stimuli were presented sequentially (either right–left or left–right, randomly interleaved) with a 600-ms interstimulus interval. The subjects were required to press one of two switches (left or right) indicating which location the first sound originated from. Following 30 presentations of these stimuli, subjects were cued by a visual stimulus to turn their head as far to the left as possible without moving their body or shoulders (approximately 90 degrees). The same speaker pairs were then tested using the same responses. Each of the possible 14 pairs of adjacent speakers were tested in two sessions in this manner for each of the three subjects.

4. Data analysis

Responses for each trial were recorded as either a (1) hit: the subject released the lever within 700 ms of the S2 stimulus onset, (2) miss: the subject did not release the lever within 700 ms of the S2 stimulus onset, (3) false-positive: the subject released the lever before the S2 stimulus offset. This time was used because it was well below the minimum reaction time on hit trials (250 ms). The false-positive rate (FP_r) was calculated for each session by the stimulus type (tone or noise) as the number of false-positive responses divided by the total number of trials for that stimulus type, regardless of the outcome of the trial. This value was used to compute the safe rate (S_r) as $(1-FP_r)$. The hit rate (H_r) was calculated as the number of hits divided by the number of hits and misses for a given stimulus type. The final performance measure (P) for a given S2 condition was calculated as $P=H_r{*}S_r$. This measure is a reliable measure of performance for safe rates above 0.85 (see Recanzone *et al.*, 1991, 1992a, 1993).

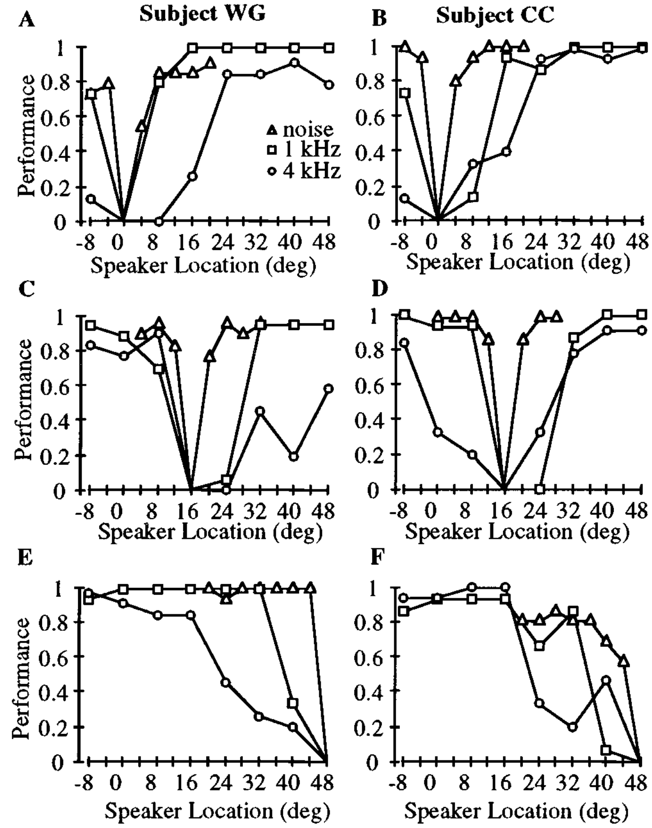

FIG. 2. Representative psychometric functions from two different subjects (WG left, CC right) at three different S1 speaker locations. Open triangles show the performance for noise stimuli, open squares show the performance for 1 kHz tone stimuli and open circles show the performance for 4-kHz tone stimuli. Psychometric functions for S1 speaker locations on the midline are shown in (A) and (B), for S1 speaker locations at 16 degrees to the right are shown in (C) and (D), and for 48 degrees to the right are shown in (E) and (F).

B. Results

Typical psychometric functions for each of the three different acoustic stimuli from three different starting S1 locations are shown for two subjects in Fig. 2. In each case, the performance measured when the S2 stimulus was presented at the same location as the S1 stimulus was zero. This is because the subjects did not detect any difference in the two stimuli (there was none), and their performance could be considered to be perfect during the ''catch'' trials. This also indicates that chance performance was very near zero, as the 18 psychometric functions of Fig. 2 represents 270 trials in which a response during a catch trial would be recorded as a hit, and neither subject recorded a hit on any of these trials. Such occurrences of responses during catch trials were very infrequent across subjects, as there were only 15 responses during 1335 catch trials (1.1%) recorded across all sessions for these three subjects.

The psychometric functions shown in Fig. 2 are representative of the data collected across subjects and sessions. The localization ability measured for the noise stimuli was consistently better than that of the tonal stimuli, and the localization ability measured for 1-kHz tonal stimuli was consistently better than the 4-kHz tonal stimuli, regardless of the S1 speaker position. To quantify this more carefully, the threshold for each S1 stimulus location was defined as the speaker separation that would give a performance value of 0.50 (Recanzone *et al.*, 1991) for changes in speaker locations both toward the midline (nasal thresholds) and away from the midline (temporal thresholds). These two threshold measurements were averaged (where possible) and plotted as a function of S1 speaker location in Fig. 3. For all three subjects, these thresholds were consistently best for noise stimuli (open triangles) which were 2–4 degrees, were somewhat worse for the 1-kHz stimuli (open squares) which were 8–10 degrees, and worst for the 4-kHz tonal stimuli (open circles) which were on the order of approximately 20 degrees (ANOVA across stimulus types for each subject, or pooled across subjects; $p < 0.01$ for both cases). These data also show that, within this frontal area of acoustic space, there is very little effect on performance or threshold as a function of distance away from the midline for any of these stimuli.

To verify that averaging the two threshold measurements was not inappropriate, we compared the thresholds measured in both directions for all psychometric functions, pooled across subjects and stimuli, in which such measurements were possible. Speaker locations at the far extremes of the region tested were not used, as only one side of the psychometric function could be measured [e.g., S1 locations at 48 degrees, see Fig. 2(E) and (F)]. These two measures did not show a statistically significant difference (paired, two-tailed t-test; $p > 0.05$).

The subjects had very low false-positive rates over the vast majority of sessions. Pooled across subjects and sessions, the false-positive rate was less than 5% in 89% of all sessions, with the greatest rate measured at 8% in one session. There was no statistically significant difference in the false-positive rates between subjects or stimulus types (ANOVA, $p < 0.001$). We interpret this to indicate that the subjects were biasing their choices to be more likely to miss an S2 stimulus than to make a false-positive response, and these threshold values may consequently be slight underestimates of the actual ability of these subjects to perform this task. This effect, however, has previously been shown to be minor given the manner in which the performance is calculated (see Recanzone *et al.*, 1991, 1992a, 1993).

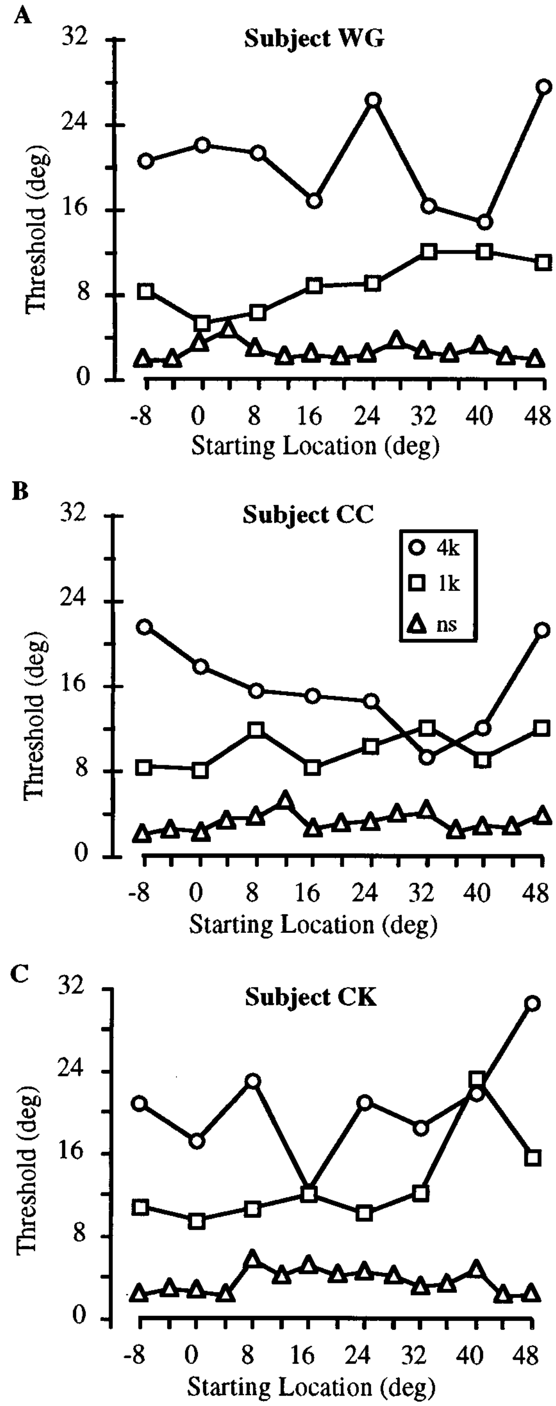

FIG. 3. Relative localization thresholds for each subject. Thresholds were calculated as the location of 0.5 performance from the psychometric functions. In cases where both the nasal and temporal sides of the psychometric function were obtained the two measures were averaged. The x axis shows the S1 speaker location. Open triangles: noise stimuli; open squares: 1-kHz tone stimuli; open circles: 4-kHz tone stimuli.

A major concern when using different speakers to measure relative localization ability is that the subjects could use speaker-specific, nonspatial cues to perform the task. Subjects were instructed to release the lever when they detected a change in the location, but could have been cueing on some other aspect of the acoustic stimulus. Although measurements of the spectrum for each speaker showed very small differences across the frequency spectrum, the stimuli were psychophysically matched across the array for each subject, and the intensity of the stimuli varied between each stimulus presentation (see Sec. II A), it is still important to ensure that nonspatial cues were not providing the subjects with additional information. To test this possibility for the tonal stimuli, similar sessions were run in which three different starting locations were used on randomly interleaved trials (0, 24, and 48 degrees). After three subjects had performed one session using the 1-kHz tone stimuli and one session using the 4-kHz tone stimuli, the speakers located at positions 8 deg and 16 degrees were exchanged, as well as the speakers located at positions 32 and 40 degrees, and the subjects were tested again the next day. We chose these speaker locations as they were along the slope of the psychometric functions for two of the three different starting speakers. If the subjects were using only spatial localization cues, the psychometric functions obtained pre- and post-exchanging the speakers should be equivalent. If the subjects used nonspatial cues, the performance for each individual speaker should be the same regardless of the speaker location.

An example of such an experiment for subject CK using the 1-kHz tone stimulus is shown in Fig. 4(A). The heavy line shows the psychometric function prior to the speaker exchange and the thin line shows the performance after speaker exchange. It is clear from this example that the two psychometric functions are nearly identical, indicating that this subject used spatial cues to perform the task. If the performance was based on nonspatial cues, the post-exchange psychometric function should have followed the dashed line. Regression analysis of the performance for each speaker before and after the exchange in location across subjects is plotted in Fig. 4(B). There is a close correspondence in performance between speaker locations regardless of which individual speaker is at that location ($r=0.922$; $p<0.0001$; slope $=0.856$). This can be contrasted with the regression analysis when the performance at each individual speaker is compared pre- and post-exchange regardless of the actual speaker location [Fig. 4(C)]. In this analysis, the correlation coefficient between the pre- and post-exchange sessions is lower ($r=0.553$) and the slope is shallower (0.514) than for the regression between speaker location, indicating again that the speaker location is the most salient cue in performing the task.

A second control addressed the same issue using noise stimuli. Since the performance for noise-stimuli was very good even for 4-degree separations, the speaker exchange paradigm could not be used. Instead we took advantage of the increase in minimum audible angle thresholds for speakers near 90 degrees compared to when the two speakers are located across the midline (Musicant and Butler, 1984; Perrott *et al.*, 1993). In this paradigm, the subjects were asked to determine which of the two speakers were activated first (left–right or right–left; see Sec. II A) when the speakers crossed the midline, and then were immediately tested after the subject turned their head approximately 90 degrees to the left. We reasoned that if there was a noticeable difference between two speakers based on nonspatial cues, the performance when the stimuli crossed the midline would be equivalent to the performance when the stimuli were far to the right. If only spatial cues could be used, the performance when the speakers crossed the midline should be much better compared to when the two speakers were near 90 degrees to the right.

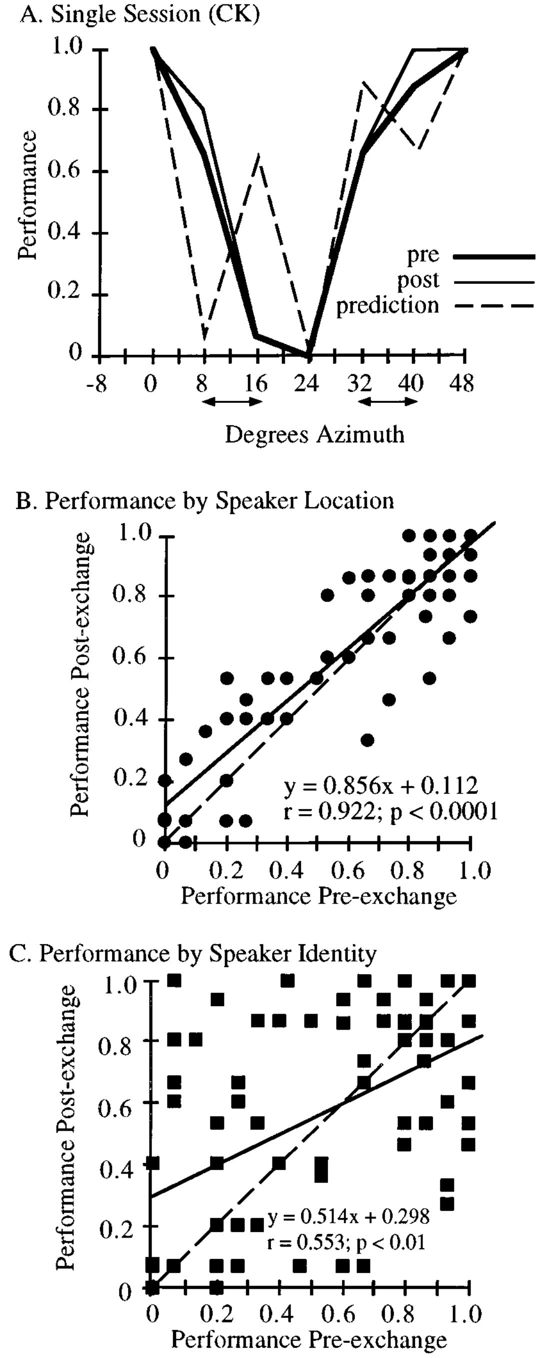

FIG. 4. Relative localization of tonal stimuli control experiments. (A) shows the psychometric functions from the session before (heavy line) and after (thin line) speakers were exchanged between locations at 8 and 16 degrees, and between locations at 32 and 40 degrees. Only the function for S1 locations at 24 degrees are shown for clarity. The dashed line represents the predicted psychometric function if the subject could discriminate between speakers using nonspatial cues. (B) Regression analysis across subjects and stimuli between the performance measured pre- (x axis) and postexchange (y axis) as a function of speaker location. Dashed line: perfect correlation. Solid line: regression line. Regression equation, r, and p values given in the inset. (C) Regression analysis as in (B) as a function of the individual speaker, regardless of spatial location. Conventions as in (B).

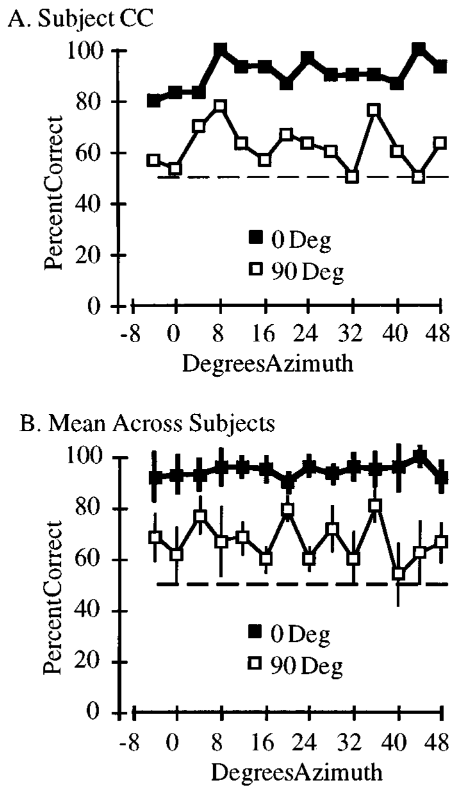

FIG. 5. Percent correct as a function of speaker location for left–right discriminations across the midline (solid squares) or at 90 degrees to the right (open squares). (A) shows the results from a single subject (CC). (B) shows the mean and standard deviations across three subjects. The dashed line indicates chance performance.

A representative example of the results of this experiment are shown in Fig. 5(A), where the solid symbols represent the performance for each speaker pair (plotted as the right speaker on the *x* axis) when the speakers crossed the midline, and the open squares show the performance when the two speakers were located approximately 90 degrees to the right. It is clear from this example that the performance is much worse with the head turned, consistent with the larger minimum audible angle at these spatial location (Musicant and Butler, 1984; Perrott *et al.*, 1993). The average data across three subjects is shown in Fig. 5(B), demonstrating that this was a consistent effect across subjects, and that there was a statistically significant difference on the performance across subjects and all speaker locations (ANOVA; $p<0.01$). These two control experiments indicate that the subjects in this report were using predominately, if not exclusively, spatial cues to perform the relative localization task.

A final concern is that subjects were improving their performance at this task as they continued to perform sessions. In every session, both noise stimuli and a tonal stimuli were presented in randomly interleaved order. To determine if there was a training effect in the two naive subjects, the thresholds for the noise stimuli are plotted as a function of the session that they were tested (Fig. 6). These data do not show any significant trends of improved performance over the first ten sessions, and performance was not statistically significantly correlated with the session number for either subject, or combined across subjects ($r<0.2$; $p>0.5$). A similar result was noted when tested with respect to the tonal stimuli. Thus, we conclude that experience had a minimal influence on the ability of these subjects to perform these tasks.

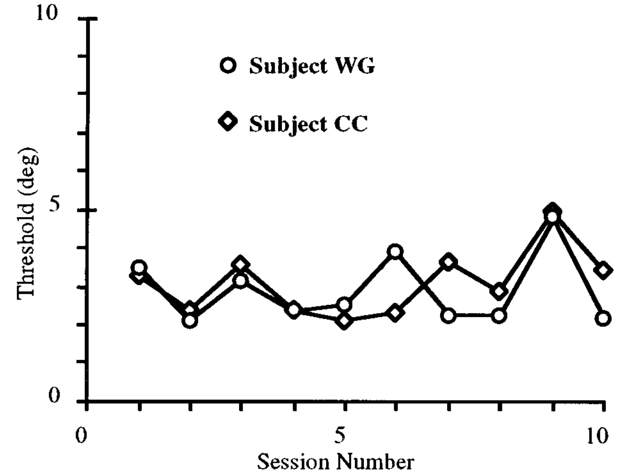

FIG. 6. No improvement in performance with practice. Thresholds for noise trials are plotted for the first ten sessions that were completed for subjects WG (circles) and CC (diamonds). Thresholds ranged from 2–4 degrees, but no significant improvement in performance over time is noted.

II. EXPERIMENT II: ABSOLUTE LOCALIZATION MEASURE

A. Methods

1. Psychophysical task

This task used the same behavioral apparatus and acoustic stimuli as the relative localization task (200-ms duration; 5-ms linear rise/fall; 30 ± 2 dB *re*: threshold; 1 kHz, 4 kHz, and Gaussian noise). The headband that the subjects wore in this task allowed horizontal head movements. The head position was measured by the current induced in a search coil located on the headband by its position in the magnetic field using standard oculomotor technology (Robinson, 1972). Subjects were signaled to orient their head at the zero position (±1 degree) by a blinking LED (Fig. 7). When this position was attained, the LED remained on continuously. One to three seconds later a single 200-ms stimulus was presented from any one of eight different speakers spanning a region of 56 degrees. In all sessions, at least one speaker location was at the midline. Subjects were required to move their head to the location they perceived the stimulus to originate from, and to maintain that position until the midline LED began to blink again (2 s from stimulus offset). All subjects consistently refrained from making returning head movements before the midline LED began to blink, which signaled the subject to reorient their head toward the midline.

Each session consisted of a single stimulus (noise, 1 kHz, or 4 kHz tone) with 21 trials for each of eight different locations (168 trials/session). For noise stimuli, a different set of eight locations were used across sessions, so that subjects were tested at all 15 locations. Subjects were not given feedback as to the accuracy of their head movements during

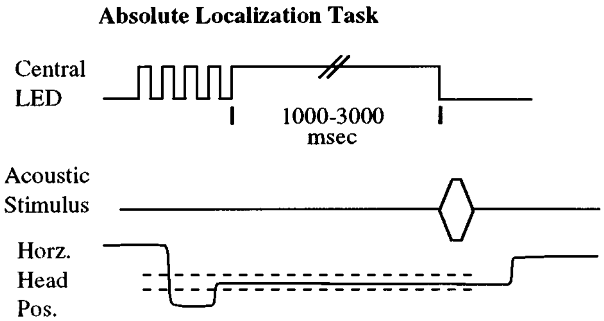

FIG. 7. Schematic of the absolute localization task. Subjects were requested to orient their head to a central flashing LED. Accomplishing this to within ±1 degree was indicated by the LED remaining continuously illuminated. A single stimulus was then presented from 1 of the 15 speakers in front of them. The subjects were instructed to turn their head to orient to the location in space that they thought the sound came from. Dashed line: electronic head position window at ±1 degree of the midline.

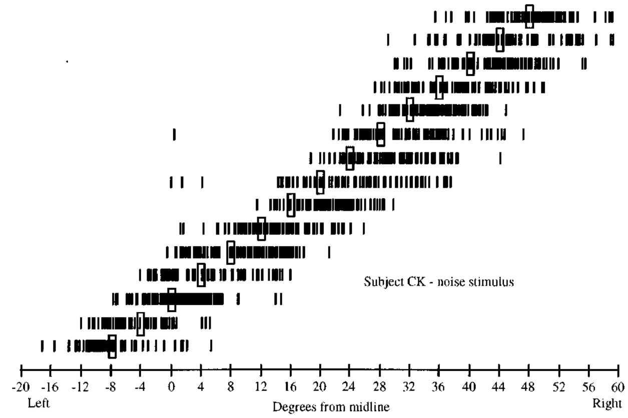

FIG. 8. Absolute localization of noise stimuli. All sessions pooled for subject CK in which the Gaussian noise stimulus was presented. Speakers were separated by 8 degrees in each session, with one speaker always located at the midline. Each small vertical line represents the final head position (estimate) of a single trial. Open rectangles show the location of the target. Each target is represented across a single row, with the rows offset vertically for clarity. The target at −8 degree (left) is shown as the bottom row, while the target at +48 degree (right) is the top most row.

the course of the session. In addition, no subjects indicated that they could visually perceive any part of the speaker array.

In order to determine the accuracy in which human subjects can orient their head to targets in general, two types of light trials were also introduced. In a ''remembered targets'' condition, a visual stimulus (LED) was blinked on for 200 ms in a manner identical to the presentation of the acoustic stimulus at one of four possible locations along the array. Subjects were instructed to orient their head to these stimuli, which were always extinguished prior to the onset of the head movement. In the ''visible target'' condition, a LED was turned on and remained on continuously for 2200 ms, again at one of four different possible locations.

2. Data analysis

Head positions were determined by the average head location measured 1950–2000 ms after the offset of the S2 stimulus (50 ms total). Inspection of the analog head movements showed that this time period was well after any minor adjustments had been made by the subjects after the initiation of the head movement (head movement equivalent to a corrective saccade) and the averaging procedure eliminated the small amount of noise from the signal.

B. Results

A representative data set for a single subject using noise stimuli is shown in Fig. 8 (CK). In this figure, the narrow vertical lines represent the final head position of a single trial. Trials for each speaker location were pooled over five sessions and plotted together. The responses for each speaker location are shown across a single row of thin lines, with the actual target location shown as the thin rectangle in each row. Targets located progressively toward the right are shown progressively offset in the y axis for clarity, but the presentation of the stimulus at each location was randomly interleaved during each session. Data were obtained at 15 different speaker locations from −8 (bottom) to +48 degrees (top) in 4-degree increments. What is most obvious from this figure is that, in spite of the fact that this subject had a relative localization threshold of 2–4 degrees for noise stimuli, the subject nonetheless made errors of the actual speaker location by up to 8–10 degrees on any given trial.

These data are representative of all subjects. Each progressively shifted their estimate toward the right for targets located toward the right. It is also evident that, although individual trials could vary over a fairly broad range, it was extremely rare for an estimate to cross into the inappropriate hemifield once the stimulus was beyond about 8 degrees from the midline. Finally, each subject tended to both overshoot and undershoot different target locations.

The absolute localization ability for the tonal stimuli is shown in Fig. 9. These data are presented in a similar manner to the noise data of Fig. 8 for the same subject (CK). In this figure, the longer rectangles show the estimates for all trials using a 1-kHz tone stimulus, whereas the shorter rectangles show the estimates of the 4-kHz tone stimuli. This subject was typical of all subjects tested, with the most salient observation that the tonal stimuli are much more poorly localized than the noise stimuli.

To quantify these data, the accuracy of the estimates was measured as the average error (average estimate-target location). All subjects showed similar errors and the mean across subjects is plotted for each target location and stimulus in Fig. 10(A). The most common error for the tonal stimuli was for the subjects to underestimate the actual target location, indicated by negative values of the mean error. Errors for noise stimuli were much smaller than those for tonal stimuli, with both overshoots and undershoots making the error very near zero. This difference between stimuli was statistically significant (noise versus 1 or 4 kHz: ANOVA, $p<0.05$). The error for localizing the 4-kHz tonal stimuli were greater than for the 1-kHz stimuli, although this difference did not reach statistical significance ($p=0.071$). Regression analysis between the error and the speaker eccentricity also did not show a statistically significant correlation ($r=0.58$, 0.06, and

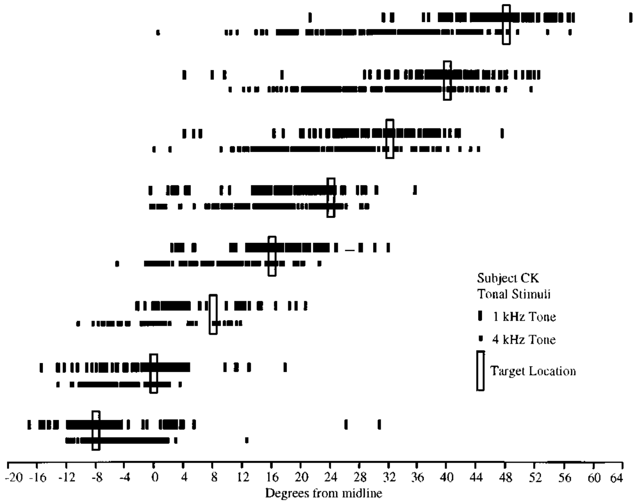

FIG. 9. Absolute localization of tonal stimuli by subject CK. Each row shows the estimates for a single target location. Long rectangles are the single trial estimates when the 1-kHz tone stimulus was presented (top set of lines for each row), the shorter rectangles are the single trial estimates when the 4-kHz tone stimulus was presented. Conventions as in Fig. 8.

0.02 for noise, 1 kHz, and 4 kHz, respectively; $p>0.05$ for all cases). We take this to indicate that there is not a significant degradation in localization accuracy as a function of eccentricity over this range in frontal space.

The precision of the estimates was measured as the standard deviation of estimates for a given stimulus type and target location [Fig. 10(B)]. There was a statistically significant difference between all three stimulus types, with the noise stimulus having the lowest standard deviation and the 4-kHz tone stimulus having the greatest standard deviation (ANOVA; $p<0.01$). An interesting observation is that the standard deviation of the estimates to noise stimuli was approximately 5 degrees, even though these same subjects routinely made correct responses to 4-degree separations in the relative localization task. Similarly, the range increased to almost 10 degrees for 1-kHz tonal stimuli, and were often even greater for 4-kHz tonal stimuli.

One apparent trend from the functions of Fig. 10(B) is that the standard deviation of the range of estimates increased with increasing eccentricity of the stimulus. This was tested quantitatively by performing a regression analysis between the standard deviation and the degrees of eccentricity of the target. All three stimuli showed a statistically significant correlation, with r values of 0.851, 0.942 and 0.903 for noise, 1-kHz tone, and 4-kHz tone, respectively. The slopes of the regression line were quite shallow, 0.066, 0.105, and 0.129 for noise, 1-kHz tone, and 4-kHz tone, respectively. These slopes indicate that even though there is a correlation between these two measures, the standard deviation of the estimates increases only approximately 1 degree for every 10 degrees that the target is moved away from the midline across the frontal region of space.

One possible explanation why the range of estimates and the accuracy were much worse than would be expected based on the relative localization results, particularly for that of the noise stimuli, is that these subjects were simply not very accurate or precise at moving their heads in the dark to the

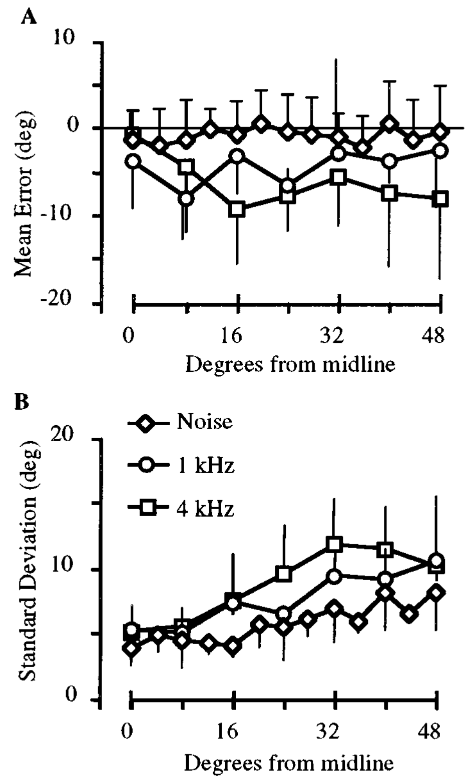

FIG. 10. Averaged errors and standard deviations across subjects. Part (A) shows the average error for noise (diamonds) 1-kHz tones (circles) and 4-kHz tones (squares) measured across subjects and target locations. Points under the dashed line represent underestimates of the targets. Thin lines indicate standard deviations. Part (B) shows the standard deviations of the estimates averaged across subjects for each of the three stimuli at each target location. Thin lines show the standard deviation of this measure.

appropriate location. It may be that many of the errors described for the noise stimuli are due to errors in head orientation, although this would still mean that the localization of tonal stimuli is less accurate and precise than for the noise stimuli. To test this possibility, we also measured head movements to continuous (2200-ms duration) and flashed (200 ms) visual targets. The averaged errors pooled across at least eight sessions for these trials is shown for all subjects in Table I. All subjects were able to localize the continuous visual stimuli to within approximately 1 degree. Only one of the four subjects was statistically significantly more accurate localizing the continuous visual stimuli compared to the flashed visual stimuli (two-tailed t test; $p<0.001$). For all subjects, the error during both brief and continuous visual stimuli was statistically significantly smaller than for the same spatial locations using noise stimuli (ANOVA, $p<0.001$ for all subjects).

Given that we were pooling responses across sessions for each of the subjects, and that it was possible that the subjects could be showing an improvement in performance over the course of these sessions, we compared the mean error calculated across stimulus locations from session to session. As subjects CK and AS were already highly experienced at this and similar psychophysical tasks, we reasoned that any training effects would have long since been established, so the analysis was confined to subjects CC and WG

TABLE I. Errors of visual trials. The means and standard deviations of the difference between the estimate and the actual target location for stimuli pooled across at least eight sessions for two classes of visual stimuli. The LED stimuli remained illuminated throughout the duration of the trial (2200 ms, column 2) or were presented for the same duration as the acoustic stimuli (200 ms, column 3). The fourth column shows the p value comparing the two visual stimuli for each individual subject (two-tailed t test). The fifth column compares the errors for the 200-ms visual stimulus to the errors of the 200-ms noise stimulus (two-tailed t test).

Subject	2200 ms	200 ms	Visual p value	ns vs vis p value
WG	-0.11 ± 2.30	0.22 ± 4.23	$p=0.112$	$p<0.001$
CC	1.15 ± 3.00	1.15 ± 5.56	$p=0.101$	$p<0.001$
CK	-0.04 ± 3.99	-0.03 ± 3.16	$p=0.223$	$p<0.001$
AS	-0.80 ± 3.70	0.86 ± 3.51	$p<0.001$	$p<0.001$

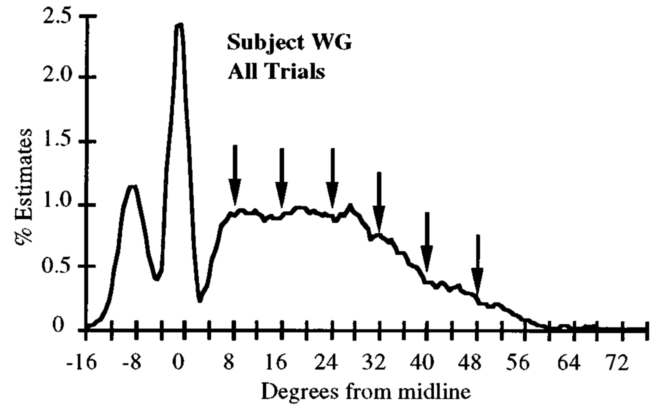

FIG. 11. Cumulative estimates pooled across sessions. All estimates recorded throughout all session were pooled (3882 total trials) for subject WG and plotted as a percentage of total trials in 0.5-degree bins. The general form of this curve, with two distinct peaks followed by a long period in which the percentage of estimates were similar and then ultimately trailing off to zero with a shallow slope, was observed in all subjects. Arrows indicate the location of targets used for both tone and noise stimuli at eight or more degrees to the right of the midline.

as they had just completed the relative localization task, and were performing this type of task for the first time. There was not a measurable learning effect for either subject over the first six sessions (repeated measures ANOVA; $p>0.10$), and no statistically significant difference was noted between any particular speaker location or pooled across speaker locations between the first and sixth session for either subject (two-tailed t test; $p>0.05$). Thus, as in the relative localization task, there was no improvement in performance across sessions for these subjects performing the absolute localization task.

A second consideration is that we used the same intensities as those in the relative localization task, which varied over a 4-dB range. It is possible that, due to the orientation of the speakers, and the random probabilities that different intensities were used, that some bias resulted. To test this possibility, one subject (AS) performed the noise absolute localization task at five different base intensity levels, again with each stimulus randomly presented ±2 dB for each base intensity. A comparison of both the mean error and the standard deviation showed a statistically significant effect only for stimuli presented 10 ± 2 dB threshold, while both measures remained constant for intensities of 20, 30, 40, and 45 ± 2 dB *re*: threshold across locations (repeated measures ANOVA; $p>0.10$). These results indicate that there is essentially no effect of intensity over this range on either of these localization measures.

The final potential source of artifact that we considered was that subjects might make a mental map of the speaker array, and would therefore create a response bias for particular locations in space. This would ultimately result in making the absolute localization task a multiple-alternative forced choice task. Given that most subjects were tested on well over 3500 trials over the course of the study, it is possible that such position biases would occur. For each subject we pooled all sessions and determined the percentage of total trials wherein responses fell within 0.5-degree bins across the full range of estimates. An example from subject WG is shown in Fig. 11. This plot shows a clear response bias at around 8 degrees to the left and for the midline, with very few estimates located to the immediate left and right of the midline. The overall shape of this curve was consistent across subjects, with only the particular locations for each peak and trough that varied by 2–3 degrees. The peak at the midline reflects the poor localization for tonal stimuli presented near the midline. Often the subjects did not perceive these tonal stimuli to originate 8 degrees from the midline, so made no head movement, resulting in the large percentage of estimates at this location (see also Fig. 9). The peak of responses to the left of the midline also probably reflects the subject's knowledge that there was only one possible leftward location during tonal sessions, and only two possible leftward locations for noise sessions. Thus, when the sound was perceived to originate from the left of the midline, most subjects made a head movement to one of the two possible locations. The low percent of estimates immediately left and right of the midline also reflects the subject's knowledge that the next possible location was a few degrees from the starting position, so never made head movements of 1–2 degrees. What we were most concerned with, however, is the possibility that the subjects had response biases at greater eccentricities to the right, where most of the stimuli were presented. For all subjects, this region was relatively flat, and there was no indication that particular locations were selected more often than any others. We also performed a fast Fourier transform over the region beyond 8 degrees for all subjects, and there was no indication of a periodicity of these estimates that would reflect a mental ''map'' of the speaker array in any subject.

III. COMPARISON BETWEEN RELATIVE AND ABSOLUTE LOCALIZATION PARADIGMS

The main goal of this study was to determine the relationship between the relative and absolute localization paradigms, which seemed to differ significantly across stimulus types. One of the most straightforward comparisons is between the region comprising $\pm$ one standard deviation of the range of estimates during the absolute localization task to an equivalent measure for the same target location in the relative localization task. For the relative localization measure

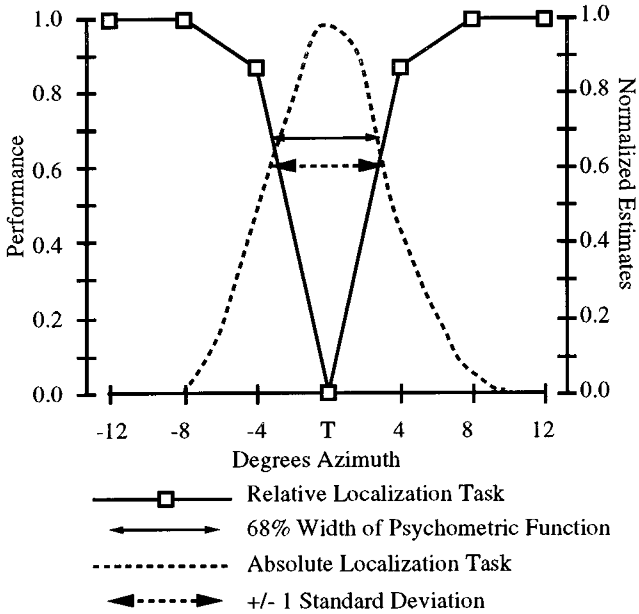

FIG. 12. Method of comparing the relative localization psychometric functions to the distribution of estimates in the absolute localization task: The psychometric function for a noise stimulus presented from a S1 speaker location at 16 degrees in the relative localization task in subject CC (open squares) is plotted with the normalized range of estimates (dashed line) for the same speaker location in the same subject. The normalized estimates were taken as a percentage of estimates in 0.5-degree bins and normalized to the peak. This distribution was shifted to be aligned with the psychometric function. The arrows show the range in degrees for the 0.68 bandwidth of the psychometric function (solid thin arrow) and the (+) and (−) 1 standard deviation for the range of estimates in the absolute localization task (thick dashed arrow). These values were used in the regression analysis shown in Fig. 13(A).

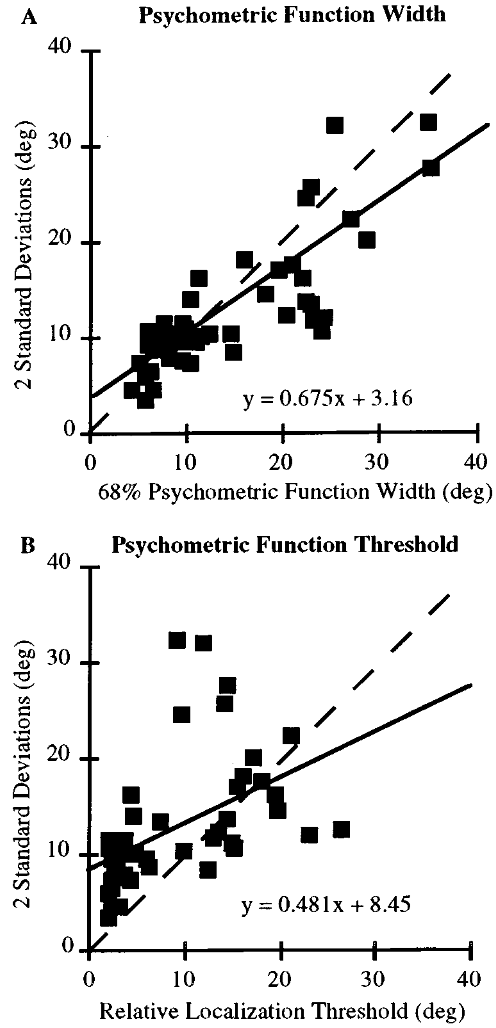

FIG. 13. Correlation between relative and absolute localization data. (A) The distance in degrees across the psychometric function at the 0.68 performance level (x axis) was plotted against two times the standard deviation of estimates for the same target location in the absolute localization task (y axis). Data were pooled across subjects and stimuli ($r=0.752$; $p<0.001$). (B) The same behavioral data as in (A) except the threshold (0.5 performance) for the relative localization task is plotted against the bandwidth measure of the absolute localization task ($r=0.501$; $p<0.001$).

we chose the width of the psychometric functions at 0.68 performance (Fig. 12). This width was chosen as it reflects the area under a Gaussian at ± one standard deviation about the mean. It is reasonable to assume that the neuronal information of stimulus location provided to these subjects is in the form of a Gaussian (Green and Swets, 1966; Hartmann, 1989), and the distribution of estimates in the absolute localization task were largely Gaussian in shape (Fig. 12—dashed line). For all psychometric functions in which the this width could be measured, the distance between the 0.68 performance values when the S2 stimulus moved temporally and nasally was calculated. This procedure limited the sample to the S1 speaker locations between 8 and 32 degrees for tonal stimuli and between 0 and 40–44 degrees for noise stimuli, as a 0.68 performance value could not be determined for speakers beyond this range both nasally and temporally. These values were then plotted against the distance of two standard deviations for the range of estimates for that same S1 speaker location. The results are shown in Fig. 13(A), combining both tonal and noise stimuli and pooled across the three subjects that completed both tasks for all stimuli (CK, CC, and WG). The dashed line is drawn through the origin with a slope of 1.0 and represents perfect correlation. This scatter plots show a good correlation between these two values that is statistically significant ($r=0.813$; $p<0.001$), with the width of the relative localization psychometric functions somewhat greater than would be predicted by the standard deviation of the range of estimates in the absolute localization task, resulting in the slope of the regression line of 0.674.

A second comparison that we made was between this standard deviation measure from the absolute localization task to the relative localization thresholds measured for the same subject and stimulus condition [Fig. 13(B)]. In this analysis, the regression coefficient was smaller (0.501) but was nonetheless significant ($p<0.001$). The slope of this regression line was also much lower (0.481) and, as can be seen from the regression plot, the relative localization thresholds were commonly much lower than would be predicted by the standard deviation measure of the absolute localization task, indicated by most points falling above the line showing perfect correlation. Thus, even though the range of estimates for a particular location in absolute space is several-fold greater than would be predicted by the relative localization threshold, the width of the relative localization psychometric function is well within the range of the estimates of target locations measured in the absolute localization task across both acoustic stimuli and individual subjects.

IV. DISCUSSION

Our relative localization results from noise stimuli are in general agreement with previous studies using a minimum audible angle procedure in normal human listeners employing noise or click stimuli (Perrott and Saberi, 1990; Chandler and Grantham, 1992; Perrot *et al.*, 1993) with similar thresholds and no apparent difference in localization thresholds as a function of distance from the midline over this limited range (Musicant and Butler, 1984; Perrott *et al.*, 1993). The relative localization thresholds obtained in this study for the tonal stimuli are either in agreement (e.g., 1 kHz, Terhune, 1985) or slightly larger than those described in previous studies (e.g., Chandler and Grantham, 1992; Molino, 1974; 4 kHz; Terhune, 1985). Differences between these studies are most likely due to differences in the intensity and duration of the acoustic stimuli, the randomly interleaved trials, and potentially the elimination of absolute loudness cues used in this paradigm.

The results of this report are also consistent with those of others using an absolute localization paradigm (Stevens and Newman, 1936; Newton, 1983; Oldfield and Parker, 1984; Butler, 1986; Perrott *et al.*, 1987; Wightman and Kistler, 1989; Makous and Middlebrooks, 1990; Middlebrooks, 1992; Butler and Musicant, 1993; Wenzel *et al.*, 1993; Good and Gilkey, 1996), particularly with respect to the 1-kHz tone being more easily localized than the 4-kHz tones (Stevens and Newman, 1936). In the most similar studies employing head movements to measure localization ability, subjects showed errors and standard deviations similar to those of this study for noise stimuli (Wightman and Kistler, 1989; Makous and Middlebrooks, 1990). In a similar study using narrow-band stimuli ($\frac{1}{6}$ octave), subjects showed a greater range of estimates and less accuracy (Middlebrooks, 1992) compared to noise stimuli, similar to the results of our subjects when comparing tonal to noise stimuli. The performance for the 4-kHz tones was also in general agreement with previous studies (Perrott *et al.*, 1987) although for most subjects the range of estimates for the 4-kHz tones was greater than previous studies using band-passed stimuli centered at 4 kHz (Abel *et al.*, 1978). This discrepancy is most likely due to the increased spectral content and longer durations of their stimuli compared to the stimuli used in this study.

In the experiments reported here, three different acoustic stimuli were used: noise, 1-kHz tones and 4-kHz tones. We chose these three stimuli because the goal of the study was to directly compare the ability to determine a change in the location of a stimulus to the ability to determine the absolute location of the stimulus. The subjects showed very different localization ability for these three different acoustical stimuli, which allowed for a comparison between these two behavioral measures across a broad range of performances. We obtained a good correlation between the width of the psychometric functions measured in the relative localization task and the standard deviations of the absolute localization task. Most points of comparison fell near a line through the origin with a slope of 1.0. Those points that fell significantly off the line were due to a larger width of the psychometric function from the relative localization task than would be expected from the standard deviation measured in the absolute localization task. This is probably due to two reasons, the first being that our measure of relative localization ability may have underestimated the subject's true localization abilities. This would be expected from the low false-positive rates, which may be reflecting the subject's bias toward more miss responses. The second is that the relative localization measurements were taken based on 15 trials for each stimulus location, and therefore were more influenced by the normal variance in each subject's performance. The absolute localization measurements were based on at least 105 trials for each speaker location for each stimulus, and were presumably less affected by this normal variance.

We considered the possibility that the subjects were able to use nonspatial cues, such as differences in the speaker transformation functions, to perform the relative localization task, but feel that this is very unlikely for several reasons. First, the thresholds we obtained were similar to those using a single speaker, as noted above. Second, these stimuli were based on each individual subject's threshold for that stimulus at that location, and all speakers were subjectively matched in intensity by each subject before the experiments were initiated. Third, we introduced a variance in the intensity of each stimulus, thereby making each stimulus sound slightly differently and forcing the subject's to concentrate on the spatial location of the stimuli during the task. Last, the control experiments described in Figs. 4 and 5 demonstrate that nonspatial cues provide very little information, if any, for the subjects to perform the task. These four factors taken together indicate that the subjects were using location cues almost exclusively in performing the relative localization task to the tonal and noise stimuli.

One interesting finding is that there was essentially no learning effect over the course of the experiment for either the relative localization task or the absolute localization task. This is a bit curious in that improvements in performance with training is a hallmark of most psychophysical paradigms (see Recanzone *et al.*, 1992a) and can be correlated with changes in the cortical representations of the relevant stimulus parameters (Recanzone *et al.*, 1992b, c, 1993; Nudo *et al.*, 1996). In the absolute localization task, subjects were not given any feedback as to either the actual speaker location or to the orientation of their head. It is therefore not surprising that there was no demonstrable improvement, as the subjects would not have any information about the nature of their error that they could use to adjust their performance. In the relative localization task, however, subjects were given feedback on a trial-by-trial basis. Subjects were aware of miss trials as the stimuli stopped being presented even though the subject never released the lever. Subjects were also indicated of false-positive trials by a longer delay between releasing the lever and the initiation of the next trial. Even with this feedback, the subjects did not show any improvement in performance over time. In data shown for one subject, significant improvement in performance at a minimum audible angle task was demonstrated over five blocks of 500 trials using an 8-kHz tone stimulus (Terhune, 1985). A likely explanation for the lack of any training effect in the relative localization task of this study is that a different starting speaker was used for each session (240 trials), so any perceptual gains that could have been acquired on the preceding session may not transfer across acoustic space. A similar lack of transference after a single session where visual stimuli are presented in a different location in the visual field have been noted in human psychophysical studies (e.g., Fahle *et al.*, 1995). It remains to be seen if continued practice at the same locations of acoustic space would generate an improvement in performance.

The most interesting finding of this study is the close correspondence between the widths of the psychometric functions in the relative localization task and the spread of the estimates in the absolute localization task. The fact that this correlation holds up for the three different acoustic stimuli, and the three subjects tested, which all had idiosyncratic localization ability, shows this relationship to be robust. If one assumes that the neuronal representation of these different speaker locations is Gaussian across a population of neurons, and that adjacent locations in space are represented by adjacent and overlapping populations of neurons, then signal detection theory predicts broader absolute localization ability than minimum audible angle thresholds, but similar widths of the two functions (Green and Swets, 1966), and supports the hypothesis that relative localization tasks, such as the minimum audible angle task, are reflecting an absolute localization strategy (Hartmann, 1989).

The representation of acoustic space in the mammalian brain is currently poorly understood (Middlebrooks and Pettigrew, 1981; Imig *et al.*, 1990; Rajan *et al.*, 1990; Middlebrooks *et al.*, 1994; Brugge *et al.*, 1996). It seems clear that the auditory cortex is necessary to localize sounds in the contralateral hemisphere (Neff *et al.*, 1956; Heffner and Masterton, 1975; Heffner, 1978; Kavanagh and Kelly, 1987; Jenkins and Merzenich, 1984; Heffner and Heffner, 1990), yet the spatial selectivity of single neurons are very broad, with only a small subset of neurons with spatial selectivity on the order of 20–40 degrees (see references cited above and Eisenman, 1974; Benson *et al.*, 1981; Ahissar *et al.*, 1992). The results of this study indicate that the measures of the range of estimates in the absolute localization task are within a factor of 2 of the most spatially selective cortical neurons reported in the anesthetized cat and monkeys. Given the current interest in the cortical contributions to sound localization as well as to the cortical contributions to auditory perception in the primate in general (e.g., see Middlebrooks *et al.*, 1994; Clarey *et al.*, 1995; Wang *et al.*, 1995; Brugge *et al.*, 1996; Barone *et al.*, 1996; deCharms and Merzenich, 1996; Stricanne *et al.*, 1996; Rauschecker *et al.*, 1997), the finding that relative localization thresholds are a poor predictor of the absolute localization ability is very important. Any studies that attempt to directly relate the responses of cortical neurons to perception, for example by single neuron spatial selectivity, population responses, or temporal coding schemes, must be careful in interpreting data based only on relative localization thresholds (i.e., minimum audible angle measurements).

V. SUMMARY

The experiments of this report describe the ability of normal human listeners to localize three different acoustic stimuli using two different behavioral paradigms. As was expected from previous, similar studies, subjects were better able to localize noise stimuli than tonal stimuli. This was true whether the subjects were tested on a relative localization task or an absolute localization task. Although it would initially appear that the ability to determine the absolute location of an acoustic stimulus was much worse than the ability to determine a change in the location of the same acoustic stimulus, these two psychophysical measures were in good agreement when the width of the psychometric function from the relative localization task was compared to the bandwidth of the range of estimates in the absolute localization task. These data indicate that the sound localization ability of normal human listeners is consistent with the spatial receptive field sizes of cortical neurons recorded in other species.

ACKNOWLEDGMENTS

The authors wish it thank M. Phan and P. Geiger for their insightful suggestions during the course of these experiments, and for reviewing previous versions of this manuscript along with M. Sutter, K. O'Connor, and W. Loftus. Funding provided by NIH Grant No. NIDCD DC0271-01A2, the Klingenstein Foundation, and the Sloan Foundation (all to GHR).

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