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The acuity of echolocation: Spatial resolution in the sighted compared to expert performance

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Abstract

Compared with the echolocation performance of a blind expert, sighted novices rapidly learned size and position discrimination with surprising precision. We use a novel task to characterize the population distribution of echolocation skill in the sighted and report the highest known human echolocation acuity in our expert subject.

Keywords

Spatial Perception; Auditory Perception; Blindness; Perception; Echolocation

Introduction

Echolocation is a specialized application of spatial hearing that uses reflected auditory information to localize objects and represent the external environment. While documented extensively in non-human species such as bats and dolphins (e.g., Harley, Putman, & Roitblat, 2003; Simmons, Moffat, & Masters, 1992; Thomas, Moss, & Vater, 2004), its use by some blind humans as a navigation and object identification aid has received far less attention. Echolocation helps these individuals with navigation and goal-directed action, object recognition, and texture perception.

The basis for these functions lies in the ability's spatial resolution, as conceived in Figure 1. Without sufficient spatial resolution, recognizing objects, surfaces, and scenes, as well as navigation, becomes difficult or impossible. This principle is similar to that articulated for visual processing (Marr, 1982) and auditory models (Slaney, 1998).

Historically, empirical research on human echolocation has focused on the blind (e.g., Ammons, Worchel, & Dallenbach, 1953; Kellogg, 1962; McCarty & Worchel, 1954; Rice & Feinstein, 1965; Supa, Cotzin, & Dallenbach, 1944), while the extent to which echolocation abilities are accessible to *sighted* subjects remains a largely open question. Quantitative studies of spatial echolocation skills in the sighted are rare and have yielded equivocal results (Hausfeld, Power, Gorta, & Harris, 1982; Kellogg, 1962; Rice, 1969; see Table 1). Stoffregen and Pittenger (1995) suggest that some form of echolocation may serve as a routine, albeit subliminal, perceptual aid for sighted as well as blind individuals, but note that the literature is sorely lacking in this regard, especially for sighted subjects.

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Tables 1a and 1b outline prior echolocation studies of blind and sighted humans, though the list is not exhaustive. Table 1a includes psychophysical echolocation experiments involving self-generated echo stimuli; Table 1b includes studies in which sighted subjects performed navigation, detection, or discrimination tasks of a passive or nonspatial nature. We did not include studies of electronic or mechanical sonar-based navigational aids. The evidence indicates that very few psychophysical experiments with sighted subjects have actually been conducted, especially using self-generated echo stimuli (as would be expected in an ecological context). With that constraint, only two prior studies (Kellogg, 1962; Rice, 1969) have investigated the spatial resolution of sighted subjects' echolocation, with conflicting results: Kellogg's subjects were unable to perform the task and Rice's subjects performed tasks at competent, yet inferior levels compared to blind subjects. No study of which we are aware specifically tested echolocation experts, who presumably represent the height of human echolocation performance.

For vision, a variety of acuity tests are common, especially the Snellen chart (Snellen, 1863). More powerful measures of the spatial resolution of vision are also available (Kniestedt & Stamper, 2003). Because human echolocation is often discussed as an auditory perceptual aid in navigation and object perception, it is appropriate to quantitatively investigate detection thresholds and the limits of spatial acuity it affords its practitioners. Such quantifications have been preliminarily described in blind subjects (Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965); but little is known of similar characteristics in the sighted (and, therefore, newly blind). Thus, this study will characterize quantitatively the spatial precision with which sighted subjects can echolocate. We also will directly compare the spatial resolution of echolocation in sighted novices with that of a blind expert echolocator. Our results show that some sighted individuals can learn to echolocate with extraordinary precision, approaching that of early-blind experts.

Experiment 1: Size Discrimination

The first experiment's goal was to measure echolocation and learning of echolocation in sighted subjects performing a size discrimination task. As similar tasks have been used before (Hausfeld et al., 1982; Kellogg, 1962; Rice, 1969), with mixed results, we used a size discrimination paradigm to compare to previous studies.

Methods

We conducted the experiment in a soundproof, echo-damped room. Eight healthy, neurologically normal volunteers participated. Each gave informed consent under human subjects protocols approved by the Institutional Review Board at the University of California, Davis. Participants were blindfolded and seated 33 cm from a frame supporting two flat, circular acrylic discs. The largest disc (diameter 25.4 cm)— the standard stimulus —was randomly located on the top or bottom of the display. One of the six comparison disks, ranging from 5.1 to 22.9 cm in diameter, was located in the other position (method of constant stimuli). The auditory angle (measured from the ears) subtended by the difference between the standard and comparison disk diameters in each pairing condition (Fig. 2) was manipulated within the range of 4.4° to 31.7°.

Subjects judged whether the larger stimulus was on the top or bottom (2AFC). The task was performed twice sequentially in each trial. The first, passive judgment (the "no-click" judgment) controlled for any possible ambient auditory information (Fig. 3a). For the second, "click" judgment, subjects used active echolocation: they made clicking noises with their tongues against the roofs of their mouths (self paced). Subjects were given no feedback. Each of four sessions contained 100 trials and lasted between 1 and 2 hours.

We conducted additional sessions at 33, 50 and 75 cm for a subset of four subjects after the initial four-session training period. The auditory angle differences in the 50 and 75 cm conditions ranged from 2.9° to 22.1° and 1.9° to 15.0°, respectively. The sessions were pseudorandomly interleaved.

Finally, to compare our sighted subjects' performance to that of an expert, we enlisted an echolocator who has been totally blind since infancy, taught himself to echolocate during childhood, and now teaches echolocation to blind and sighted individuals (subject EB, to maintain anonymity). To avoid ceiling effects, we tested EB exclusively at a distance of 75 cm, where angular differences between stimuli subtended from 1.9° to 15.0°. EB gave informed consent in accordance with protocols approved by the Institutional Review Board at UC Davis.

Analysis

Data from the sessions at 33 cm were analyzed in two ways. First, we tested whether discrimination improved with increasing size differences, whether clicking facilitated discrimination, and whether performance improved with training. We conducted a three-way (4×2×6) repeated-measures ANOVA with within-subjects factors of Session, Clicking (no-click vs. click) and Separation, as well as post-hoc tests (see RESULTS). Second, where possible, we fitted logistic psychometric curves (Equation 1a) to results from individual runs and group data, using Wichmann and Hill's (Wichmann & Hill, 2001a) procedure, with bootstrapped confidence intervals (Wichmann & Hill, 2001b) (see Fig. 3a for a single-session example). Threshold calculation was not possible for all sessions due to low performance on early or difficult sessions (see RESULTS below for further discussion).

Results, Experiment 1

Figure 3a shows no-click and click data for sighted subjects' first four sessions at 33 cm distance. The solid lines represent performance in the clicking condition; dashed lines represent the no-click baseline. A three-way (4×2×6) repeated-measures ANOVA with within-subjects factors of Session, Clicking and Separation revealed significant main effects of Clicking ($F_{1,7}$=44.737; p<.001) and Separation ($F_{5,35}$=6.07; p<.001). While the main effect of Session was not significant ($F_{3,21}$=1.40; p=.27), a significant Session × Clicking interaction ($F_{3,21}$=4.75; p=.011) suggests that session effects were carried by only the click condition, while no-click baseline performance remained stable. Subsequent repeated-measures ANOVAs performed separately on the no-click and click conditions confirmed this, showing a significant main effect of Session ($F_{3,21}$=3.59; p=.031) for the click condition but not for no-click ($F_{3,21}$=2.48, p=.09). No-click data collapsed over four sessions from all subjects did not differ significantly from chance (p_{Bonf} > .05 for all conditions).

Training effects were evident for the four sessions at 33 cm. Initially, subjects had great difficulty echolocating even large differences in object size. Subsequent sessions showed significant improvement, with performance markedly better after a single session and approaching asymptote after 3 sessions, as indicated by the significant effect of Session. Figure 3b emphasizes session effects as difference scores between no-click and click performance rather than raw percentages.

Representative psychometric functions for one skilled sighted observer, BL, and blind expert echolocator EB are shown in Fig. 3c. Their 75% thresholds (14.5° and 8.0°, respectively) indicate that both were proficient in discriminating size differences in single sessions. The best performances during individual sessions among sighted subjects discriminated auditory angle differences as small as 5.3° (though all subjects' average performance was coarser than EB's single-session threshold).

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Figure 4 shows pooled click data from the four observers who underwent additional sessions at larger distances; for comparison, data from EB's single size-discrimination session is shown as well. Each curve represents the averaging of three asymptotic sessions for each of four observers at the distance indicated. Regardless of the distance, performance varied along the same curve when plotted against the angular size difference, independently of linear distance. Psychometric curves fitted to group performance yielded thresholds of 16.9° at 33 cm and 19.2° at 50 cm (group performance at 75cm did not exceed 75%). Monte Carlo simulation showed the curves were not significantly different (p=.27). This suggests that thresholds are constrained by the difference in auditory angle subtended by the stimuli, rather than absolute stimulus size or distance within the range we tested. Overall, the results demonstrate that sighted subjects can learn to use echolocation to precisely discriminate object size over a range of near-field distances.

Experiment 2: Echolocation vernier acuity

The first experiment revealed that untrained sighted subjects can quickly learn to echolocate. However, it remains unclear what level of spatial precision they attain and how this compares to that of early-blind expert echolocators. Additionally, size discrimination, while a nominally spatial task, may not tap or quantify the fine-grained limits of spatial localization. To investigate whether novice sighted echolocators could approach the spatial resolution of a blind expert, we measured echolocation in an auditory version of a vernier acuity task, like that used by vision scientists (McKee & Westheimer, 1978a). A typical visual-vernier acuity task involves a pair of line segments arranged end-to-end, slightly displaced orthogonally to their orientation; subjects determine the direction of displacement on each trial (McKee & Westheimer, 1978b; Westheimer & McKee, 1977). Vernier acuity can reveal extremely fine discrimination thresholds, smaller than the width of a single photoreceptor (Westheimer, 1979; Westheimer & McKee, 1977)—the finest possible spatial resolution of perception.

Several previous echolocation studies presented single stimuli in detection or localization experiments, or pairs of stimuli in 2IFC discrimination experiments. Adapting vernier stimuli to an echo-perception domain affords us a new measure of spatial precision in echolocation, uniquely allowing us to measure relative (rather than absolute or egocentric) spatial localization. Spatial perception depends largely on relative localization, and this vernier method provides a means to characterize the resolution of auditory spatial acuity.

Methods

We used a setup similar to Experiment 1 (Fig. 5a). Sighted participants (N=11), who met the same criteria and informed consent conditions as those in Experiment 1, sat blindfolded facing the frame at a distance of 50 cm. Two vertically separated disks (20.3 cm diameter) were presented with one of five horizontal center-to-center separations from 1.1° to 13.2° of auditory angle (Fig. 5a). Using the method of constant stimuli, 20 trials on average were collected for each of five vernier separations, for a total of 100 trials per session (1–2 hours per session). Subjects reported whether the top disk was located to the right or left of the bottom disk (2AFC task). Trials were conducted and analyzed in the same general manner as in Experiment 1 (cf. Fig. 2c and Experiment 1 Methods). Each observer participated in a minimum of 5 sessions to ensure asymptotic performance.

Expert echolocator EB was available for two sessions of the vernier acuity task. Based on a running average (bin width, 10 trials), EB reached asymptotic performance in the second session. The first session was conducted at 75 cm and the second at 100 cm, to avoid ceiling effects. In the first session, EB participated in 20 trials at each of four vernier separations ranging from 0.75° to 4.5° of auditory angle. In the second session, the four vernier separations ranged from 0.57° to 3.4°. To achieve asymptotic performance as quickly as possible, all subjects were given correct/incorrect feedback after each trial (Herzog & Fahle, 1997).

Results, Experiment 2

A two-way repeated-measures ANOVA (Clicking × Separation) on all sighted subjects' data yielded a significant effect of Clicking ($F_{1,10}$=6.9; p=.025). While the effect of Separation collapsed across Clicking conditions did not reach significance ($F_{4,40}$=1,98; p=.116), the Condition × Separation interaction was significant ($F_{4,40}$=2.74; p=.042). Thus, clicking was significantly helpful to subjects, as no-click group performance never exceeded chance levels, and the effect of stimulus separation is clearly carried by the click condition. A repeated-measures ANOVA on only the click condition revealed a significant effect of stimulus separation, $F_{4,40}$=2.76, p=.041. To confirm that the effect was not driven by outlying values, we performed a nonparametric chi-square analysis on subject performance at each individual stimulus separation. A fixed-sequence, incremental application of the Bonferroni correction for multiple comparisons (Westfall & Krishen, 2001) indicated that group performance was significantly above chance levels for the two greatest separations, 6.6° and 13.2° (χ^2 = 7.36, p = .014; χ^2 = 4.46, p = .014, respectively; see Fig. 5d).

The representative plots in Fig. 5b show psychometric functions fitted to individuals' data. However, the initial group analysis belies widely varying performance among subjects and sessions (Fig. 5c), reflecting a large increase in task difficulty from Experiment 1. For example, the highest group mean performance at the widest separation (13.2°) was 63.5%, but individual subject performance at that separation ranged from 45.6% to 95.0%; i.e., some subjects were highly proficient at the task, others less so, and some failed completely. Two sighted subjects, BL and KK, performed best in the range of auditory angles we sampled, performing at above 75% correct and allowing us to compute thresholds from psychometric functions as in Experiment 1. Thresholds pooled over all sessions were 4.1° for BL and 6.7° for KK. These are the finest discriminations among sighted subjects, though not necessarily at an expert level; by comparison, EB's 75% threshold during his second session was 1.58°.

While a full comparison between sighted and blind echolocators would require a larger sample size than the present study, our results suggest that not all sighted subjects can be equally trained. Nevertheless, the results convincingly demonstrate sufficiency—some sighted subjects can achieve echolocating precision approaching that of an experienced blind echolocator.

Discussion

In two experiments, we tested the spatial resolution of the echolocation abilities of sighted control subjects and one expert blind echolocator, constraining the echo-producing vocalizations to self-generated clicks. In Experiment 1, coarse echolocation ability could be readily trained in sighted subjects, even without explicit feedback about performance; feedback did not significantly alter performance. Further, size discrimination thresholds were roughly constant with increasing distance, so angular size difference, rather than distance, may be the key metric of size discrimination using echolocation (Rice et al., 1965). Experiment 2 employed a novel and challenging vernier acuity task to precisely measure the spatial resolution of echolocation. Importantly, contrasting all previous studies, we found that with sufficient training some sighted subjects can learn to echolocate with a proficiency level that approached that of an early-blind expert echolocator.

The second experiment introduced a new measure of echolocation acuity—the vernier stimulus. This stimulus provides a means of operationally defining the acuity of echolocation, akin to the spatial acuity of vision, and potentially a basis for objective measurement and comparison across individuals and individual differences. This could be especially valuable if active echolocation becomes more prevalent as a navigational aid for the blind (Ashmead, 2008). The substantially finer resolution measured for EB and BL relative to their size-discrimination performance also suggests that while auditory vernier discrimination may be a more difficult task, it also could measure very fine spatial resolution in echolocation.

Comparison to previous studies

Previous studies did not definitively measure the acuity or spatial resolution of echolocation in sighted individuals (Table 1). As discussed earlier, Rice (1969) and Kellogg (1962) were closest but published conflicting results. Kohler (1964) recruited many sighted participants for his investigations of auditory orienting but tested *passive detection* of obstacles and not spatial discrimination. Experiments with blindfolded sighted subjects tested shape discrimination with no explicit spatial component and no measure of acuity (Hausfeld et al., 1982). Arias and Ramos (1997) and Arias et al. (1993) tested repetition pitch, a proposed echolocation cue (Bassett & Eastmond, 1964), in sighted subjects but did not explicitly test spatial resolution nor the perception of self-generated echoes.

The considerable performance variability in the present study may help explain the varying results in prior work. The distribution of echolocation ability in normally hearing, sighted subjects ranges from complete inability to near-expert thresholds (Experiment 2) and varies with specific echolocation tasks (Experiment 1 vs. 2). The small numbers of subjects in previous studies could have produced inconsistent patterns of results that reflect this distribution. Future investigations of, e.g., the underlying cues used in echolocation should leverage the individual differences present in echolocation ability.

Training echolocation

Table 1 shows that most previous echolocation studies focused on the performance of blind subjects, with training potential as an implied motivation of the research. We show that some naïve sighted subjects with relatively limited training can approximate the spatial resolution of an expert with several decades' worth of experience; all sighted subjects in our study achieved at least a coarse ability to echolocate (Experiment 1). Not all subjects reached this level of precision (Experiment 2); however, it is not clear that all blind subjects can echolocate equally either without a substantially larger population of randomly sampled blind subjects than has been tested previously (rarely more than 6 per study). Minimum thresholds achieved by some of our sighted subjects over relatively few sessions in Experiment 1 approached those reported previously for blind subjects (Kellogg, 1962; Rice et al., 1965), though performance by EB. It is noteworthy that EB had spatial acuity and size discrimination thresholds that rivaled or exceeded the spatial resolution of all previous estimates in the literature using self-generated cues, as well as previous estimates of auditory spatial resolution involving passive listening to noise stimuli (Blauert & Allen, 1997).

Echolocation per se, therefore, is not a rare ability practiced by a few skilled individuals; the crucial spatial resolution component of the skill, while not immediately accessible to most untrained subjects, can be readily learned. Objective measures of echolocation acuity, like our vernier technique, are critical to evaluating training programs of the type offered by EB; our results therefore hold promise for such programs geared to newly blind individuals.

Conclusions

We have characterized the spatial resolution of novice and expert human echolocation using size discrimination and novel relative spatial localization tasks. We show rapid perceptual learning of echolocation without feedback and that some sighted individuals can be trained in echolocation to a level of precision that approaches that of early blind expert echolocators. The developmental time course of echolocation skills and their neural correlates in blind and sighted individuals, and the characterization of the most important echolocation cue(s), remain fertile avenues for future research. Pragmatically, orientation and mobility as well as echolocation research and training programs should consider including adults with recent blindness.

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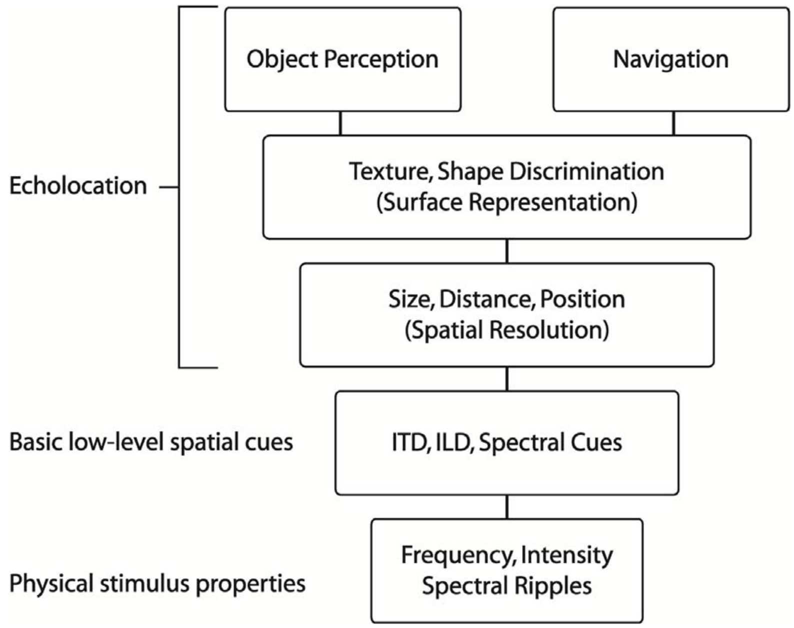

Figure 1.
Proposed five-level, inverted-pyramid representational framework for various levels of cues comprised by echolocation. First level of analysis: physical stimulus properties, such as sound frequency, intensity, or spectral ripples from reflections. Second level of analysis: low-level spatial hearing cues, such as interaural time and level differences and spectral transformation cues. These are analyzed to perform the basic functions subserved by spatial hearing and build toward the third level of analysis: spatial resolution, including the perceived size, distance and position of objects. Fourth level of analysis: surface representations, such as texture and shape. These, in turn, give rise to fifth-level analyses such as successful object perception and navigation. Spatial resolution information afforded by aural cues, investigated in the present study, marks the lowest level in this scheme at which echolocation occurs. See main text for additional details.

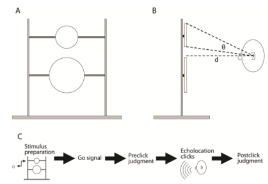

Figure 2.
Setup and trial sequence for Experiment 1. Front (A) and lateral (B) views of the echolocation stimulus setup. Two vertical wooden dowels of diameter 6.35mm were mounted on a rectangular wooden base, connected by two flat aluminum crossbars, which supported the stimulus disks. Subjects sat at distance *d* (33, 50 or 75 cm) from the vertical plane formed by the stimuli; from this, the auditory angle θ subtended by targets was calculated. Each trial began with an immediate response without clicking, after which the subject began clicking and then made a second judgment (C). Responses were verbal, consisting of the words “top” or ‘bottom” to indicate where the larger disk was perceived.

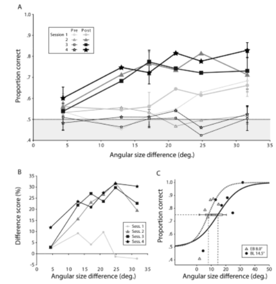

Figure 3.
Experiment 1 results. Panel (A): Size-discrimination performance for 8 sighted subjects over 4 sessions at a distance of 33 cm. Two curves are plotted for each of 4 sessions: one for no-click (open circles, dashed lines) and one for click (echolocation) judgments (filled circles, solid lines). No-click judgments did not exceed chance performance. Click judgment performance increased reliably with angular difference, from chance levels at 4.4° to over 80% at 31.7° in session 4. Error bars represent SEM. Panel (B): Difference scores (click minus no-click) showing the performance benefit of echolocation increasing across sessions. Four curves represent difference scores for 4 sessions. Session 1 indicates negligible benefit, while sessions 2, 3 and 4 show clear perfomance benefits of up to 30%. Panel (C): Comparison of two individual psychometric functions and 75% discrimination thresholds calculated from single-session performances of expert subject EB (distance 75 cm) and sighted subject BL (distance 33 cm). Thresholds were 14.5° for BL and 8.0° for EB. Horizontal error bars represent bootstrapped 95% confidence intervals.

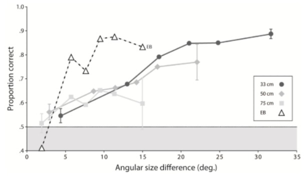

Figure 4.
Distance effects on size discrimination. Plot showing size-discrimination performance averaged across 4 sighted subjects at 3 different distances: 33, 50 and 75cm. Solid curves represent asymptotic performance (averaged over 3 sessions) for 4 subjects at distances of 33 (circles), 50 (diamonds) and 75 cm (squares). The three curves line up well. Expert EB's single-session data at 75cm is shown for comparison. Representative error bars indicate SEM. Thresholds estimated from pooled subject data performance were 16.9° for 33 cm and and 19.2° for 50 cm. Large uncertainty in 75% thresholds for lower performance precluded curve fitting for 75 cm sessions. The background region shaded for clarity indicates performance regime below 50% correct.

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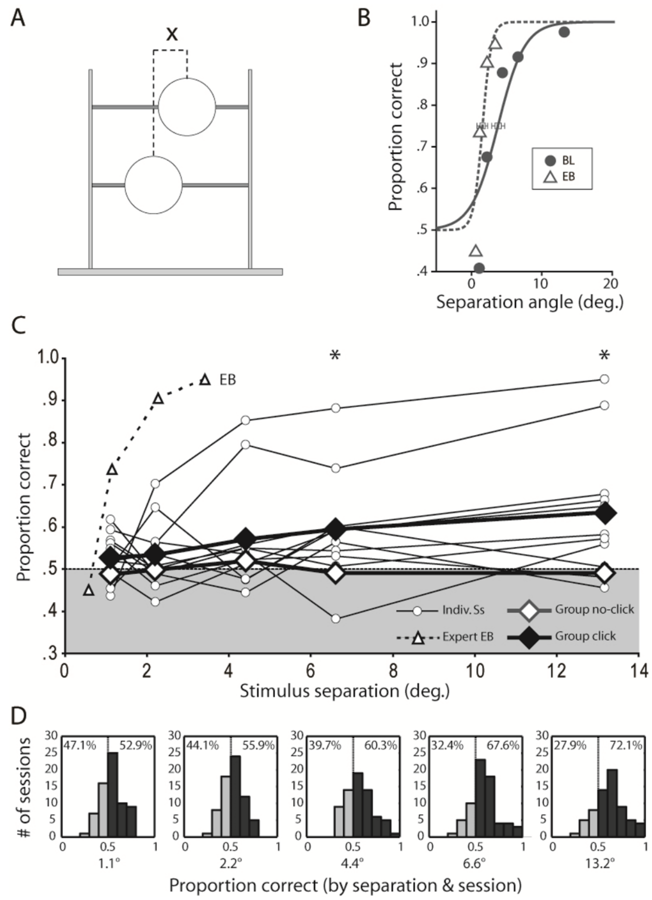

Figure 5.

Stimulus setup and results of Experiment 2. Panel (A): Vernier experiment setup. Equal-sized stimuli were displaced horizontally from a central axis; the total horizontal displacement between disk centers subtended a range of auditory angles from 1.1° to 13.2° (calculated as described in Fig. 2a). Panel (B): Psychometric functions showing vernier acuity for sighted subject BL and expert echolocator EB. The function for BL represents the average of four sessions at a distance of 50cm. EB's vernier acuity was measured at a distance of 100 cm. The 75% threshold was 1.58° separation between stimuli for EB and 3.76° for BL. Panel (C): Group plot of Vernier discrimination performance, with separate curves for each sighted subject, in addition to curves for group click and no-click performance. Solid diamonds indicate sighted subjects' group no-click performance, at chance for all separations. Open diamonds indicate group click performance, which was above chance. Click performance of individual sighted subjects is indicated by open circles. For comparison, open triangles indicate single-session data from expert echolocator EB (not included in group averages). Shaded background region indicates performance regime below 50% correct. Asterisks above 6.6° and 13.2° separations indicate significant ($p < .05$) chi-square results comparing subjects scoring above vs. below 50% correct at each separation. (D) Histogram of performances across all sessions by sighted subjects at each stimulus separation. Dark shading indicates sessions in which performance was above 50% correct. Percentages indicate proportion of sessions with performance above or below 50% at each separation.

Table 1
Previous Studies of Blind and Sighted Echolocation

Prior echolocation studies testing echolocation in sighted humans. A. Studies in which a spatial discrimination task, involving the active self-generation of echoes, could be used to estimate a threshold. B. Studies in which subjects performed only navigation, passive listening, or nonspatial tasks. Numbers of subjects separated by plus signs indicate subjects in separate experiments within a study.

Study	Blind subjects	Sighted subjects
a. Spatial resolution estimated from active self-generated echoes		
Kellogg, 1962	2	2
Welch, 1964	0	0
Rice et al., 1965	5	0
Rice & Feinstein, 1965	4	0
Rice, 1967	5+4+6+4	0
Rice, 1969	6+8	8+3
Ashmead, Hill, & Talor, 1989	10+15	0
b. Navigation, passive, and nonspatial discrimination tasks		
Supa et al., 1944	2	2
Cotzin & Dallenbach, 1950	2	2
Worchel & Berry, 1952	0	15
Ammons et al., 1953	0	20
Kohler, 1964	0	267+20+48
Bassett & Eastmond, 1964	0	1
Clarke, Pick, & Wilson, 1975	8	8
Juurmaa & Suonio, 1975	10	5
Hausfeld et al., 1982	1	18+18+45
Strelow & Brabyn, 1982	8	14
Boehm, 1986	5	11
Rosenblum, Gordon, & Jarquin, 2000	0	20+26
Hughes, 2001	0	5+10+20+11
Doucet et al., 2005	12	20
Despres, Candas, & Dufour, 2005	0	15+30
Dufour, Despres, & Candas, 2005	12	20
Schenkman & Nilsson, 2010	10	10