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The Acuity of Echolocation: Spatial Resolution in Sighted Persons Compared to the Performance of an Expert Who Is Blind

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Abstract: Compared with the echolocation performance of an expert who is blind, sighted novices rapidly learned size and position discrimination with surprising precision. We used a novel task to characterize the population distribution of echolocation skills in sighted persons and report the highest-known human echolocation acuity in the expert who is blind.

Echolocation is a specialized application of spatial hearing that uses reflected auditory information to localize objects and represent the external environment. Although it has been documented extensively in nonhuman species, such as bats and dolphins (see, for example, Harley, Putman, & Roitblat, 2003; Simmons, Moffat, & Masters, 1992; Thomas, Moss, & Vater, 2004), its use by some persons who are blind as a navigation and object-identification aid has received far less attention. Echolocation helps these individuals to navigate their environments, to engage in goal-directed action, to recognize objects, and to perceive textures.

The basis for these functions lies in the spatial resolution provided by the practice of echolocation, as conceived in Figure 1. Without sufficient spatial resolution, it is difficult or impossible to recognize objects, surfaces, and scenes and to navigate the environment. This principle is similar to that articulated for visual processing (Marr, 1982) and auditory models (Slaney, 1998).

Historically, empirical research on human echolocation focused on people who were blind (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 persons remains a largely open question. Quantitative studies of spatial echolocation skills in sighted individuals are rare and have yielded equivocal results (Hausfeld, Power, Gorta, & Harris, 1982; Kellogg, 1962; Rice, 1969).

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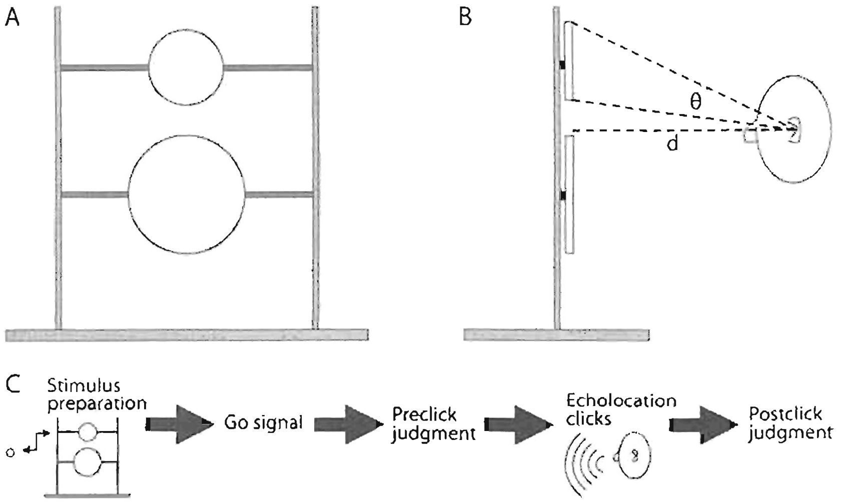

Figure 2. Setup and trial sequence for Experiment 1. Front (A) and lateral (B) views of the echolocation stimulus setup. Each trial began with an immediate response without clicking, after which the participant began clicking and then made a second judgment (C).

13 inches) from a frame supporting two flat, circular acrylic discs. The largest disc, with a diameter of 25.4 centimeters (about 10 inches)—the standard stimulus—was randomly located on the top or bottom of the display. One of the six comparison disks, ranging from 5.1 centimeters (2 inches) to 22.9 centimeters (about 9 inches) 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 diameters of the standard and comparison disk in each pairing condition (see Figure 2) was manipulated within the range of 4.4 degrees to 31.7 degrees.

The participants judged whether the larger stimulus was on the top or bottom in what is known as a two-alternative forced choice task (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 (see Figure 3A). For the second, "click," judgment, the participants used active echolocation, that is, they made clicking noises with their tongues against the roofs of their mouths (self-paced). The participants were given no feedback. Each of four sessions contained 100 trials and lasted between one and two hours.

We conducted additional sessions at 33, 50, and 75 centimeters (about 12 inches, 20 inches, and 30 inches, respectively) for a subset of four participants after the initial four-session training period. The differences in the auditory angle in the 50- and 75-centimeter conditions ranged from 2.9 degrees to 22.1 degrees and 1.9 degrees to 15.0 degrees, respectively. The sessions were pseudorandomly interleaved.

Finally, to compare the sighted participants' performance to that of an expert, we enlisted an echolocator (EB, to maintain his anonymity) who has been totally blind since infancy, taught himself to echolocate during childhood, and now teaches echolocation to individuals who are blind and sighted. To avoid ceiling effects, we tested EB exclusively at a distance of 75 centimeters, where angular

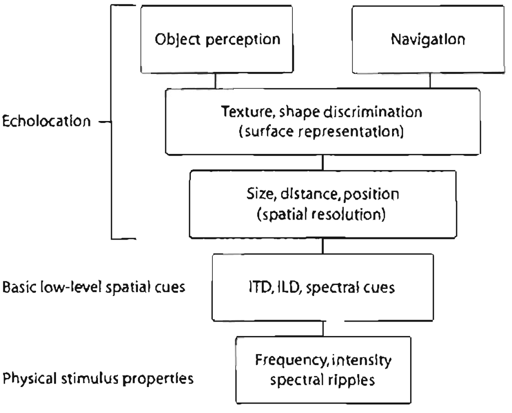

Figure 1. Proposed five-level, inverted-pyramid representational framework for various levels of cues comprised by echolocation. ITD = interaural time differences; ILD = interaural level differences.

Stoffregen and Pittenger (1995) suggested that some form of echolocation may serve as a routine, albeit subliminal, perceptual aid for sighted as well as blind individuals, but noted that the literature is sorely lacking in this regard, especially for sighted persons.

Tables 1 and 2 outline prior studies of echolocation in persons who are blind and those who are sighted, although the list is not exhaustive. Table 1 includes psychophysical echolocation experiments involving self-generated echo stimuli; Table 2 includes studies in which sighted persons performed navigation, detection, or discrimination tasks of a passive or non-spatial nature. We did not include studies of electronic or mechanical sonar-based navigational aids. The evidence indicates that few psychophysical experiments with sighted persons have 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) investigated the spatial resolution of sighted persons' echolocation, with conflicting results: Kellogg's participants were unable to perform the task, and Rice's participants performed tasks at competent, yet inferior, levels compared to participants who were blind. 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

Table 1
Previous studies of echolocation by blind and sighted participants: Spatial resolution estimated from active self-generated echoes.

Study	Blind participants	Sighted participants
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

Note: The number of participants separated by plus signs indicates participants in separate experiments within a study.

Table 2
Previous studies of blind and sighted echolocation: Navigation, passive, and nonspatial discrimination tasks.

Study	Blind participants	Sighted participants
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

Note: The number of participants separated by plus signs indicates participants in separate experiments within a study.

appropriate to investigate quantitatively detection thresholds and the limits of spatial acuity that human echolocation affords its practitioners. Such quantifications have been preliminarily described in participants who are blind (Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965), but little is known about similar characteristics in persons who are sighted (or newly blind). Thus, the study presented here quantitatively characterized the spatial precision with which sighted persons can echolocate. We also directly compared the spatial resolution of echolocation in sighted novices with that of an expert echolocator who is blind. Our results show that some sighted individuals can learn to echolocate with extraordinary precision, approaching that of experts who become blind early in their lives.

Experiment 1: Size discrimination

The goal of the first experiment was to measure echolocation and the learning of echolocation in sighted participants who performed a size-discrimination task. Because 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 our results to those of 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, as did the expert who is blind. The participants were blindfolded and seated 33 centimeters (about

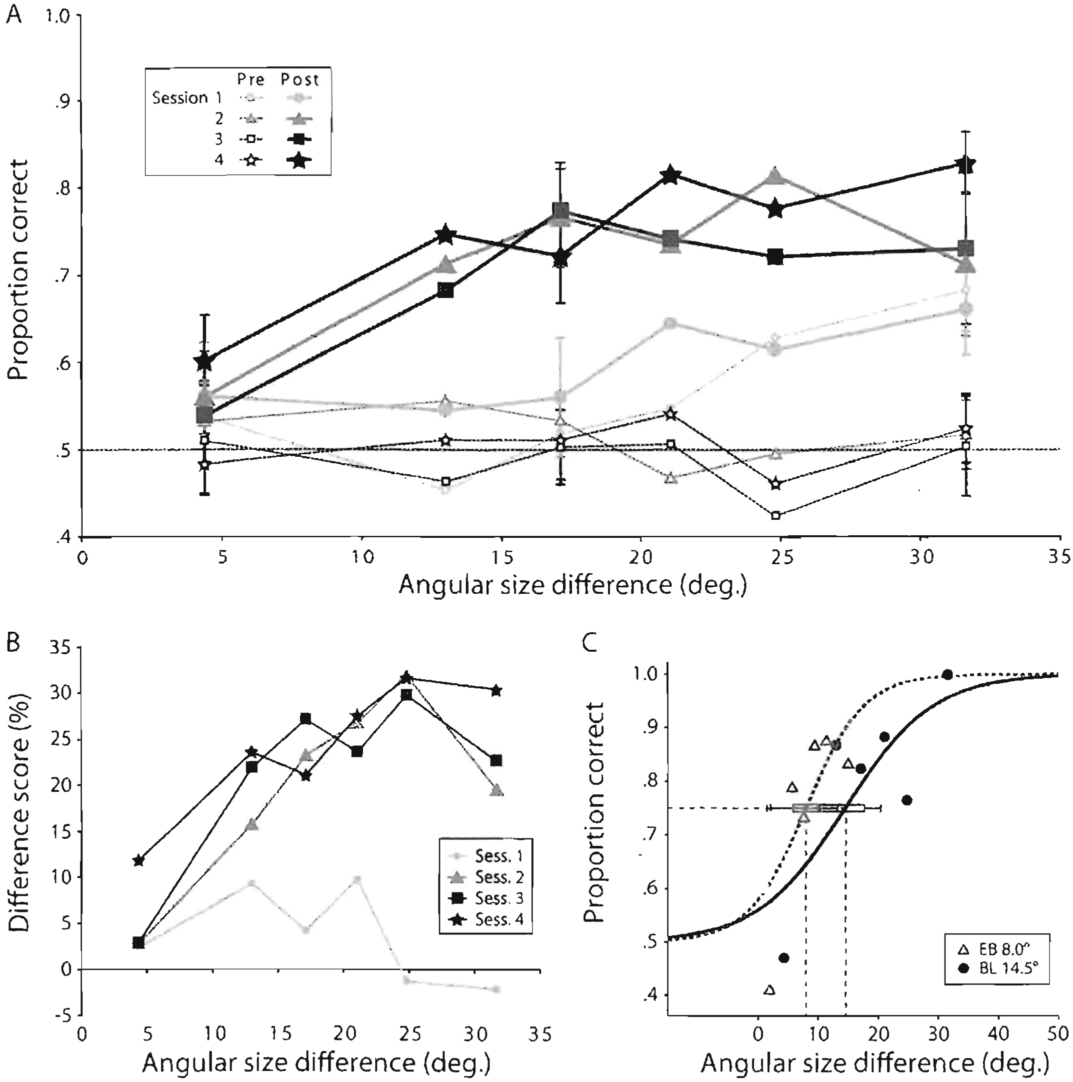

Figure 3. Results of Experiment 1. Panel (A): Size-discrimination performance for 8 sighted subjects over 4 sessions at a distance of 33 centimeters. Error bars represent SEM. Panel (B): Difference scores (click minus no-click) showing the performance benefit of echolocation increasing across sessions. Panel (C): Comparison of two individual psychometric functions and 75% discrimination thresholds calculated from single-session performances. Horizontal error bars represent bootstrapped 95% confidence intervals.

differences between stimuli subtended from 1.9 degrees to 15.0 degrees.

Analysis

Data from the sessions at 33 centimeters were analyzed in two ways. First, we tested whether discrimination improved with increasing sizes, whether clicking facilitated discrimination, and whether performance improved with training. We conducted a three-way (4 × 2 × 6) repeated-measures analysis of variance (ANOVA) with within-subjects factors of session, clicking (no-click versus click) and separation, as well as post-hoc tests (see the Results for Experiment 1). Second, where possible, we fitted logistic psychometric curves to results from individual runs and group data, using Wichmann and Hill's (2001a) procedure, with bootstrapped confidence intervals (Wichmann & Hill, 2001b) (see Figure 3A for a single-session example). It was not possible to calculate thresholds for all the sessions because of the participants' low performance on early or difficult sessions.

Results, Experiment 1

Figure 3A shows the no-click and click data for the sighted participants' first four sessions at a distance of 33 centimeters. The solid lines represent performance in the clicking condition; the 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 ($F_{5,35} = 6.07$; $p < .001$). Although 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, whereas the no-click baseline performance remained stable. Subsequent repeated-measures ANOVAs that were performed separately on the no-click and click conditions confirmed this finding, showing a significant main effect of session ($F_{3,21} = 3.59$; $p = .031$) for the click condition but not for the no-click condition ($F_{3,21} = 2.48$, $p = .09$). The no-click data collapsed over four sessions from all participants did not differ significantly from chance ($p_{Bonf} > .05$ for all conditions).

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

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

Figure 4 shows pooled click data from the four observers who underwent additional sessions at larger distances; for a 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 degrees at 33 centimeters and 19.2 degrees at 50 centimeters (group performance at 75

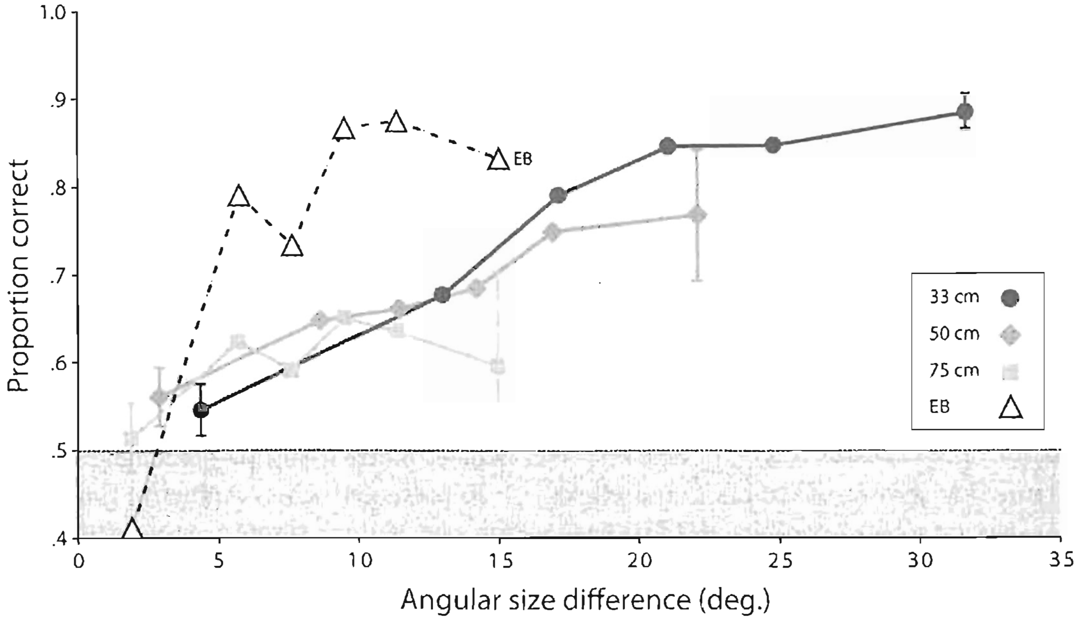

Figure 4. Distance effects on size discrimination. Representative error bars indicate SEM.

centimeters did not exceed 75%). Monte Carlo simulation showed that the curves were not significantly different ($p = .27$). This finding suggests that thresholds are constrained by the difference in the auditory angle subtended by the stimuli, rather than by the absolute stimulus size or distance within the range that we tested. Overall, the results demonstrate that sighted persons can learn to use echolocation to discriminate precisely the size of an object over a range of near-field distances.

Experiment 2: Echolocation vernier acuity

The first experiment revealed that untrained sighted participants can quickly learn to echolocate. However, it remains unclear what level of spatial precision they attain and how this level compares to that of expert echolocators who are congenitally blind. In addition, 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 an expert who is blind, we measured echolocation in an auditory version of a vernier acuity task, like that used by vision scientists (McKee & Westheimer, 1978). A typical visual-vernier acuity task involves a pair of line segments arranged end to end, slightly displaced orthogonally to their orientation; participants determine the direction of displacement on each trial (McKee & Westheimer, 1978; 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 studies of echolocation presented single stimuli in detection or localization experiments or pairs of stimuli in 2IFC (two-interval forced choice) discrimination experiments. Adapting vernier stimuli to an echo-perception domain afforded 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 (see Figure 5A). Eleven sighted participants, who met the same criteria and informed-consent conditions as those in Experiment 1, sat blindfolded facing the frame at a distance of 50 centimeters. Two vertically separated disks of 20.3 centimeters each in diameter or about 8 inches) were presented with one of five horizontal center-to-center separations from 1.1 degrees to 13.2 degrees of auditory angle (Figure 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). The participants 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. Each observer participated in a minimum of five sessions to ensure asymptotic performance.

Expert echolocator EB was available for two sessions of the vernier acuity task. On the basis of a running average (bin width, 10 trials), EB reached asymptotic performance in the second session. The first session was conducted at 75 centimeters and the second at 100 centimeters (about 39 inches) to avoid ceiling effects. In the first session, EB participated in 20 trials at each of four vernier separations ranging from 0.75 degrees to 4.5 degrees of auditory angle. In the second session, the four vernier separations ranged from 0.57 degrees to 3.4 degrees. To achieve asymptotic performance as quickly as possible, all the participants were given correct or incorrect feedback after each trial (Herzog & Fahle, 1997).

Results, Experiment 2

A two-way repeated-measures ANOVA (clicking × separation) on the data for all the sighted participants yielded a significant effect of clicking ($F_{1,10} = 6.9$; $p = .025$). Although 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 the participants because the no-click group's 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 the participants' 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 degrees and 13.2 degrees ($\chi^2 = 7.36$, $p = .014$; $\chi^2 = 4.46$, $p = .014$, respectively; see Figure 5D).

The representative plots in Figure 5B show psychometric functions fitted to

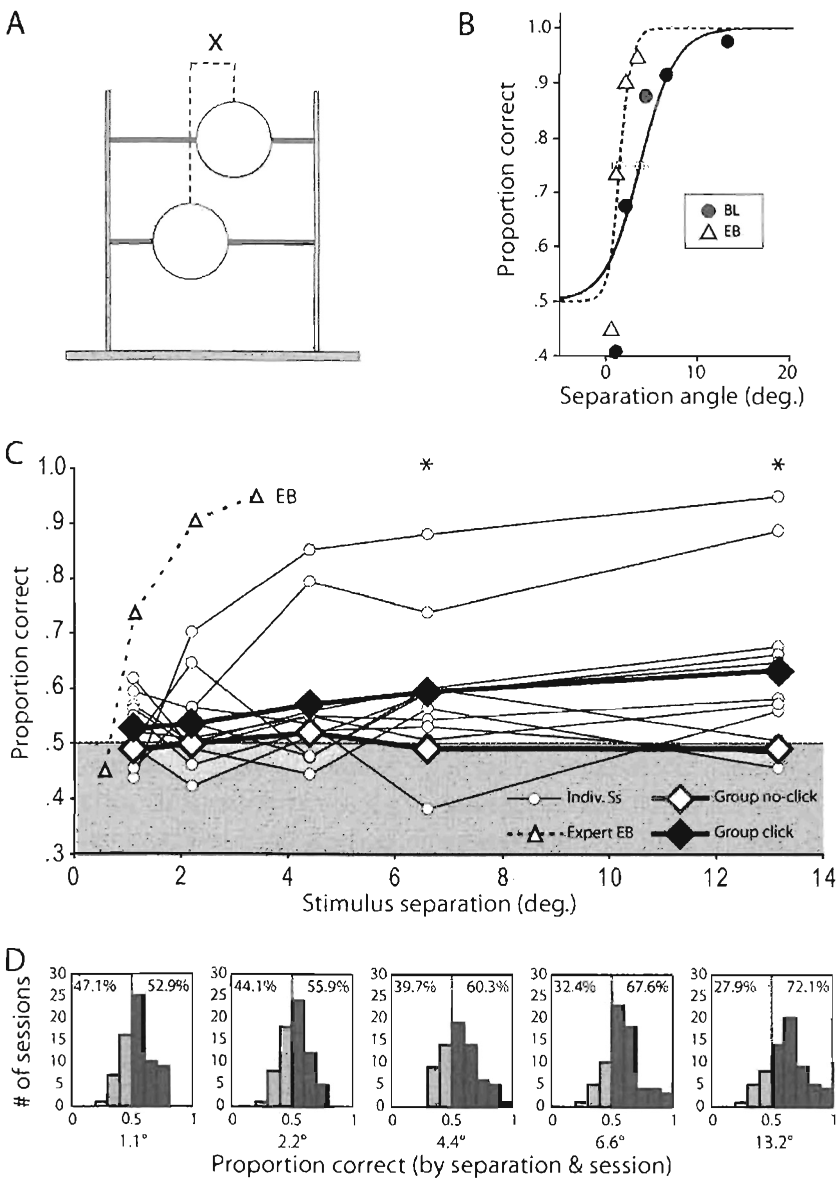

Figure 5. Stimulus setup and results of Experiment 2. Panel (A): Vernier experiment setup. Panel (B): Psychometric functions showing vernier acuity for sighted participant BL and expert echolocator EB. Panel (C): Group plot of Vernier discrimination performance. Panel (D): Histogram of performances across all sessions by sighted participants at each stimulus separation. Indiv. Ss = individual subjects or participants.

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

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

Discussion

In two experiments, we tested the spatial resolution of the echolocation abilities of sighted participants and one expert echolocator who is blind, constraining the echo-producing vocalizations to self-generated clicks. In Experiment 1, the sighted participants could be readily trained in coarse echolocation ability, even without explicit feedback about their performance; feedback did not significantly alter their performance. Furthermore, size-discrimination thresholds were roughly constant with increasing distance, so the difference in the size of the angle, rather than distance, may be the key metric of size discrimination using echolocation (Rice et al., 1965). Experiment 2 used a novel and challenging vernier acuity task to measure the spatial resolution of echolocation precisely. An important finding, which differed from those of all previous studies, was that with sufficient training some sighted persons learn to echolocate with a level of proficiency that approaches that of expert echolocators who are congenitally blind.

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. It could be especially valuable if active echolocation becomes more prevalent as a navigational aid for individuals who are blind (Ashmead, 2008). The substantially finer resolution measured for EB and BL relative to their size-discrimination performance also suggests that although auditory vernier discrimination may be a more difficult task, it also could measure 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 (see Table 1). As we 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, not spatial discrimination.

Experiments with blindfolded sighted subjects tested the discrimination of shapes with no explicit spatial component and no measure of acuity (Hausfeld et al., 1982). Arias and Ramos (1997) and Arias, Curet, Moyano, Joekes, and Blanch (1993) tested repetition pitch, a proposed echolocation cue (Bassett & Eastmond, 1964), in sighted persons but did not explicitly test spatial resolution or the perception of self-generated echoes.

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

Training echolocation

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

Thus, echolocation per se is not a rare ability practiced by a few skilled individuals; the crucial spatial resolution component of the skill, although not immediately accessible to most untrained persons, 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 that are geared to individuals who are newly blind.

Conclusions

We have characterized the spatial resolution of novice and expert human echolocation using size discrimination and novel, relative spatial localization tasks. We showed that perceptual learning of echolocation can be rapid without feedback and that some sighted individuals can be trained in echolocation to a level of precision that approaches that of expert echolocators who are congenitally blind.

The developmental time course of echolocation skills and their neural correlates in individuals who are blind and sighted and the characterization of the most important echolocation cues remain fertile avenues for future research. Pragmatically, research and training programs in both orientation and mobility and echolocation should consider including adults who have recently become blind.

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