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By

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Abstract

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The use of active natural echolocation as a mobility aid for blind humans has received increased scientific and popular attention in recent years (Engber, 2006; Kreiser, 2006; NPR, 2011), in part due to a focus on several blind individuals who have developed remarkable expertise. However, perhaps surprisingly, the history of empirical human echolocation research is not much younger than the era of echolocation research (cf. Griffin, 1958). Nevertheless, compared to its bat and cetacean counterparts (Thomas et al., 2004), the field today remains in a state of comparative infancy. Until quite recently, nearly the entire body of human echolocation research has been behavioral in nature, with little insight into perceptual and neural mechanisms.

Thus, the goal of this manuscript is to broadly integrate research findings in human echolocation across time, levels of analysis, and methodology. We will define human echolocation as it has been operationalized in research and practice, review behavioral goals served by echolocation, and identify putative auditory cues and neural mechanisms underpinning human echolocation. We examine some individual differences in echolocation performance, particularly involving blind compared to sighted persons. We present two studies in detail, addressing the spatial acuity of echolocation skills in sighted volunteers and blind experts. Throughout, we identify outstanding theoretical and applied questions that may form the basis for ongoing and future research. Taken together, we conclude that echolocation can serve behaviorally relevant perceptual goals; that spatial echolocation tasks such as size discrimination can be learned by sighted subjects, not just the blind; that the spatial resolution of echolocation can rival that of peripheral vision; that the variegated cues driving echolocation performance are processed at multiple levels of the auditory system; and that blindness likely plays an important role in shaping individual differences in echo processing.

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David Whitney, advisor/chair

Contents

1. Introduction

How do blind and visually impaired people interact with a dynamic external world? Everyday tasks of navigation and object perception are rendered prosaic by a functional visual system. In its absence, these tasks become considerably more challenging. Often, nonvisual sensory modalities such as somatosensation and audition assume increased importance as they fill roles usually dominated by vision (Kupers and Ptito, 2013; Pascual-Leone et al., 2005). In this context, we consider active echolocation, in which practitioners interpret the reflected information from emitted acoustic pulses, as a remarkable example of a means of gaining information about the world.

Echolocation: Active sampling at a distance

A precise definition of human echolocation has eluded consensus. Most broadly, it is the perception of acoustic echoes by humans. Here, we primarily consider *active* echolocation, which involves self-generated vocalizations employed in the service of orientation, navigation and object perception. Unlike passive hearing of sound sources, active echolocation provides information about silent objects, i.e., auditory information about environmental features that do not themselves emit sound. Additionally, fittingly for an active sensory modality, auditory information from active echolocation is strongly dependent on pulses generated by the observer, unlike ambient sound fields in reverberant spaces, which can also be informative for navigation but do not require sound production by the observer (Ashmead and Wall, 1999; Ashmead et al., 1998). Furthermore, unlike haptic exploration, active echolocation can sample the environment beyond the direct sampling available in peripersonal space. For purposes of context and comparison, we will consider instances of passive echo processing, and echo pulses generated externally and/or artificially (Rice, 1967; Schenkman and Jansson, 1986; Schenkman and Nilsson, 2010).

2. Historical overview

The bulk of human echolocation research to date comprises high-level, behavioral investigations, in laboratory settings as well as naturalistic environments. Systematic study of the acoustic cues and mechanisms recruited for echoic perception has only emerged relatively recently, often informed by advances in non-human echolocation research.

Finding an auditory basis for the obstacle sense

The history of human echolocation finds its origins intimately bound with the centuries-old history of skillful navigation and object perception in blind persons. Consider the "blind man of Puisaux" described in Enlightenment philosopher Denis Diderot's 1749 "Letter on the Blind" (Diderot, 1916). He navigated city streets with apparent ease and localized sounds and objects with great precision. While the blind man of Puisaux commonly begins most historical overviews of human echolocation, including the present one, it is important to note that Diderot does not mention active signals generated by the blind man. Rather, the blind man of Puisaux evinces the so-called "obstacle sense" or "facial vision," umbrella terms which would come to be replaced as the nature of echolocation was further investigated. Two excellent reviews covering the subsequent two centuries (Hayes, 1935; Supa et al., 1944) detail several other cases, and attempted explanations, of successful navigation and object perception in blind travelers. For most of that time, even the most general underlying mechanism of the obstacle sense was unknown, perhaps partly because blind persons themselves are often equally unable to describe accurately the bases of their obstacle judgments (Cotzin and Dallenbach, 1950; Kish, 2003; Supa et al., 1944; Worchel and Dallenbach, 1947). Hayes (1935) catalogued over a dozen explanatory hypotheses spanning auditory, tactile, and more exotic modalities (e.g., disturbances in an ether-like "od"), among which active echolocation found little purchase. Diderot himself attributed the blind man of Puisaux's navigational skills to cutaneous tracking of air pressure, writing that he judged "the proximity of bodies by the action of the air on his face. He is so sensitive to the least atmospheric change, that he can distinguish between a street and a closed alley" (Diderot, 1916, p. 78).

Modern experimental studies of the obstacle sense and the basis for understanding active human echolocation began in the 1940s with Karl Dallenbach's series of studies conducted at or affiliated with Cornell University (Ammons et al., 1953; Cotzin and Dallenbach, 1950; Supa et al., 1944; Worchel and Dallenbach, 1947). The general design of the so-called Cornell studies probed the detection and localization of large obstacles (walls and movable screens) by subjects walking along an indoor or outdoor path. The most fundamental overall contribution of the Cornell studies was to establish definitively the auditory basis of the obstacle sense. Subjects with their ears plugged (Ammons et al., 1953; Supa et al., 1944), or deaf subjects (Worchel and Dallenbach, 1947), were consistently unable to detect and avoid large obstacles in their path, while various non-aural manipulations did not hinder subjects with unimpeded hearing. In this basic task, blindfolded sighted subjects could also learn to avoid obstacles. The differences between blind and sighted persons performing the same tasks remain an active topic of research, with a complex picture of the two groups' relative abilities emerging (see Kupers and Ptito, 2013 for an excellent overview), and will be an ongoing theme throughout this manuscript.

Active echolocation

The advent of research into bat and cetacean echolocation in the 1950s and 1960s (e.g. Griffin, 1958; Norris et al., 1961) yielded a new series of studies of increasing precision and rigor, with interest explicitly focused on the sensitivity of active echo perception. Studies by Kellogg (Kellogg, 1962) and Rice (Rice, 1967, 1969; Rice and Feinstein, 1965; Rice et al., 1965) provided much of these new data, which are among the first true psychophysical studies of active human echolocation. Kohler (1964) quantified the benefits of active echo emissions to the obstacle sense versus passive listening to ambient sounds. He openly criticized the continued use of the term "obstacle sense," as it implied a sensory modality separate from existing senses, when its auditory basis had been so firmly established. The terms "echolocation" and "sonar" tended to predominate from then on, though not without debate over their appropriate scope. See also Stoffregen and Pittenger (1995) or Kish (2003) for excellent reviews of this period in the history of echolocation research.

Inquiry into the acoustic cues subserving human echolocation begun by Cotzin and Dallenbach (1950) continued with increasing rigor, investigating not only audition at different frequencies but also the contributions of frequency difference thresholds (Carlson-Smith and Wiener, 1996; Kohler, 1964), variation in ambient sound fields (Ashmead and Wall, 1999), various signal spectra (Schenkman and Jansson, 1986), Doppler frequency shifts, and repetition pitch (Bassett and Eastmond, 1964).

Elucidating limits, cues and mechanisms

Recent echolocation research has taken advantage of new methods, increased knowledge, and greater visibility (and availability) of trained blind echolocation practitioners. Psychophysical techniques, pioneered by Kellogg (1962) in an echolocation context, have evolved to allow for more precise measurements of spatial resolution (e.g. Teng et al., 2012), as well as increasingly precise technical manipulation of acoustic properties (Papadopoulos et al., 2011; Rowan et al., 2013; Schörnich et al., 2012; Wallmeier et al., 2013) to identify task-specific cues. Other promising technical developments, such as functional magnetic resonance imaging (fMRI), have allowed the first investigations of the physiological mechanisms underlying echolocation in humans (Thaler et al., 2011; Thaler et al., 2013). These developments are considered in greater detail below.

3. The behavioral envelope of human echolocation

Overview

Despite a proliferation of data on specific experiments, research into human echolocation has until recently been diverse, sparse, and relatively nonsystematic. Stoffregen and Pittenger (1995; p. 183) admonished that "the theoretical literature on human echolocation is scanty," which remains largely true today, owing partly to many narrowly focused, yet disparate, research efforts. So, how should we think about human echolocation? What kinds of conceptual frameworks would help to organize our thinking about of the scope and mechanisms of human echolocation? For example, a general auditory framework may invoke the classic bottom-up hierarchies for vision (Hubel and Wiesel, 1962; Marr, 1982), tracing ascending levels and complexity of sensory processing. A similar proposed framework comprises sensory cues and processing for echolocation specifically (Teng and Whitney, 2011). However, these ignore top-down processes so important to perception; Slaney (1998) outlined a bottom-up auditory framework expressly to critique such models of "pure audition." Here this bottom-up organization is revised to emphasize the behavioral functions of human echolocation; that is, what goals and tasks it may serve and the mechanisms by which they are achieved. This is similar to previous loose frameworks that comprised multiple tasks and experimental results in echolocation. Au (2004) compared bat and dolphin echolocation abilities under the rubric of six echolocation tasks involving target detection and spatial and temporal echo discrimination. Ulanovsky and Moss (2008) examined some of the numerous complex tasks faced by echolocating bats in the framework of foraging behavior.

By way of conceptually summarizing a widely divergent body of experimental literature, we can delineate a rough spatial "behavioral envelope" within which echolocation has been tested. Figures 3-1 and 3-2 provide a schematic overview of studies reporting results from obstacle and object detection and localization tasks. It should be stressed that this is not a direct quantitative comparison, as experimental procedures, measures, conditions, analyses, and subjects vary widely between studies. Nevertheless, a picture begins to emerge. For example, detection distances are clearly on a larger scale than that of spatial localizations. Long-cane taps (e.g. Schenkman and Jansson, 1986) and attention to sound fields without active echo pulses (e.g. Ashmead et al., 1998; Strelow and Brabyn, 1982) are useful in detecting obstacles for navigation but provide relatively coarse localization cues. In the following sections, key behaviorally relevant categories of echolocation performance are reviewed and summarized through major experimental findings.

Quality of life and independence

Two very basic questions often asked of active echolocation are who uses it, and whether it works. That is, does it improve a practitioner's perception, mobility, independence, and general quality of life? These questions seem basic, yet ultimately motivate more specific research into perceptual advantages afforded by echolocation. Despite this, thus far, empirical attention directed toward this higher-level question has been relatively sparse. However, in the field of orientation and mobility training for blind persons, active echolocation has gained increased recognition, primarily as a navigational aid. Reported uses of active echolocation in a survey of blind practitioners (Brazier, 2008) included obstacle detection and avoidance, as well as orientation and navigational behaviors such as “shorelining” (navigation relative to an extended feature such as a wall) and maintaining straight-line travel. Though expertise is relatively uncommon, a very recent survey of practitioners suggests that echolocation is associated with advantages in everyday life (Thaler, 2013). Practicing echolocators reported higher salaries and better mobility in unfamiliar places compared to non-echolocators.

These surveys are generally in line with more focused experimental results and abundant, though previously unconfirmed, anecdotal and popular reports. However, the sample sizes in Thaler’s (2013) and Brazier’s (2008) survey were very small (N = 37 and 10, respectively), with data comprising self-reports. Thus, while most research published to date has investigated specific aspects of echo perception, the overall impact of practicing echolocation remains open to further study.

Mobility: Navigation, orientation, and obstacle detection

Successful navigation through an environment is an essential function of daily life and thus critical to the utility of echolocation. Kish (2003), writing from an orientation and mobility viewpoint, explicitly endorses improved mobility as a goal for applied echolocation training programs.

Obstacle detection

Obstacle detection, essential to successful navigation, received a large amount of early experimental attention, principally with the Cornell studies mentioned above. Subjects would walk blindfolded along a path, indicate their “first perception” of the obstacle, then approach it as closely as possible without collision for a “final appraisal” of the obstacle’s position. Dependent measures included distances at which each of these judgments was rendered, as well as the number of trials resulting in collisions. This paradigm has remained influential in subsequent studies (Ashmead et al., 1989; Carlson-Smith and Wiener, 1996; Juurmaa, 1969).

Most of the Cornell studies did not explicitly test actively generated echo signals as a navigational aid. The chief manipulation of emitted cues involved shoes on a hardwood floor versus socks on carpet, but the intent was to test whether audition was the underlying modality of the obstacle sense, as opposed to cutaneous sensitivity to air currents or temperature or olfactory gradients. Generally, extraneous noises such as heel clicks, whistles, finger snaps — any noises not “made normally in connection with walking” (Supa et al., 1944, p. 165) — were typically forbidden to the participants. The general result was that “first perceptions” were made at varying ranges between approximately 1 – 5 m as long as subjects could hear (Cotzin and Dallenbach, 1950; Supa et al., 1944), with blind subjects typically making these perceptions at larger distances than sighted counterparts (see Figs. 3-1 and 3-2 for details). “Final appraisals” without collisions, a measure of spatial precision in the obstacle detected, remained fairly constant at about 15-25 cm, whether a wall or moveable board was being perceived (Cotzin and Dallenbach, 1950; Supa et al., 1944). Again, sighted subjects typically had larger, i.e. coarser, final appraisals, typically on the order of 30-60 cm (Ammons et al., 1953). Invariably, performance suffered whenever auditory cues were dampened or blocked, whether through replacing subjects’ shoes with socks, covering hardwood flooring with carpet runners, blocking the ears, using deaf subjects (Worchel and Dallenbach, 1947), or allowing ambient outdoor noise (Ammons et al., 1953).

In a notable exception, Cotzin and Dallenbach (1950) administered the obstacle approach task remotely using an active sound emitter: blind and sighted participants sat stationary wearing headphones, while an apparatus in a separate room approached an obstacle while emitting continuous stimuli: broadband noise or pure tones ranging from 125 Hz to 10 kHz. The best results were reported with broadband noise and the 10 kHz pure tone conditions, while pure tones at lower frequencies resulted in poor performance. The authors reported that high-frequency audition is essential to the obstacle sense, a conclusion that proved controversial in subsequent decades.

One report (McCarty and Worchel, 1954) describes a young blind subject, 11 years old and totally blind since the age of 3, who could successfully navigate around buildings and outdoor obstacles with the aid of oral clicking sounds he had developed spontaneously. Though their investigation was informal even by contemporary standards, the authors measured the subject's ability to avoid large boards set along a test track while bicycling at various speeds, finding that faster travel (up to nearly 7 m/s) did not incur more collisions. This report is among the very earliest published descriptions of active echolocation using mouth clicks. The utility of this technique is suggested in the report, though not experimentally manipulated.

By contrast, three blind participants using long-cane tapping sounds for navigation found that they could detect obstacles in their path, but only localized them crudely (Schenkman and Jansson, 1986). Asked to report their detection and localization of moveable cardboard obstacles in a design resembling that of the Cornell studies, the blind participants detected the obstacles at a mean distance of about 3.6 m but localized them to a mean distance of about 47 cm. In other words, collision rates exceeded, detection ranges were on par with, and localization was three times as coarse as, unaided blind subjects relying on footfalls for similar tasks.

Finally, it is worth noting that there are anecdotal reports of active echolocation obstacle detection ranges far exceeding the distances described above (e.g., 15 m in McCarty and Worchel, 1954; approx. 45 m in Walters, 2013). While such reports have not been experimentally verified, they constitute predictions open to testing.

Orientation and wayfinding

Some of the earliest empirical echolocation research has addressed the applied question of locomotion and orientation in blind persons. Does active echolocation, i.e., the use of self-generated oral clicks or other emitted signal, improve this critical ability over (or in concert with) other techniques? Some echo information, such as cane tapping sounds and footfalls, is used by blind people for navigation purposes. However, investigations of these cues in orientation and obstacle detection reveal the great difficulty and limited spatial utility of the "natural obstacle sense."

Strelow and Brabyn (1982) measured the accuracy of locomotion using sound cues. In a quiet carpeted room, blind and blindfolded sighted subjects attempted to travel a straight 10-m path, parallel to a “shoreline” consisting of a fiberboard wall or widely spaced thin poles. Any sounds in addition to footfalls were permitted; only physical contact with the shoreline objects was forbidden. The authors found that blind participants significantly outperformed their blindfolded sighted counterparts, with lower deviations from straightness and fewer collisions and other “gross errors.” However, the authors were manifestly unimpressed at overall levels of performance, pointing out that even the best performance by blind subjects was vastly inferior to normal sighted subjects. Strelow and Brabyn (1982) concluded that in the echo signals “there does not appear to be sufficient associated location information to guide locomotion effectively” (p. 640). Schenkman and Jansson (1986), detailed above, also doubted the spatial precision of echo signals, even when actively tapped out by long canes. Similarly, in studying auditory judgments of gap crossability, Burton (Burton, 2000) found that cane tapping sounds offered virtually no advantages in this task, and concluded that sounds alone were not enough to guide locomotion.

Rosenblum et al. (2000) blindfolded sighted subjects and asked them to echolocate the distance to a wall at varying distances. Subjects either echolocated the wall while stationary or walking toward it. After reaching a specified starting point, they walked to the spot where they had judged the wall to be. Subjects overall tended to represent a truncated space (i.e., undershooting the wall at larger distances and overshooting it at shorter distances), making errors of roughly 20-100 cm, in contrast to “final appraisal” precision of approx.. 15-25 cm in the Cornell studies. The authors also reported a weak (marginally significant) facilitatory effect of walking on echo accuracy. Another study using simulated motion when judging a sound field near a wall (Ashmead and Wall, 1999; see Chap. 6) found no evidence of a facilitatory effect from simulated self-motion. The marginal or absent support for a facilitatory effect of motion on echolocation performance stands in contrast to Cotzin and Dallenbach (1950), who implicated motion-induced Doppler cues as informing their subjects.

Ashmead and Wall (1999) presented listeners with sound fields that spectrally simulated one of two distances from a wall, additionally manipulating stimuli to simulate motion toward the wall. Subjects were able to judge which of the distances was closer at about half a meter, consistent with previous behavioral reports. The results were consistent with the authors’ model of spectral variations in ambient sound fields, i.e., passive auditory information.

Together, Ashmead and Wall (1999) and Strelow and Brabyn (1982) suggest that besides the detection of looming obstacles, the specific role played by active echolocation in locomotive orientation and navigation remains somewhat underexplored. Likely, the utility of active echolocation depends on specific situations in which reflected auditory emissions can provide more spatial or object information than reflections from ambient sound fields.

Interestingly, one of Schenkman and Jansson’s (Schenkman and Jansson, 1986) subjects, eliminated for “cheating” by using oral sounds counter to instructions, performed considerably better than the mean. Kish (2003) speculates that oral clicks and cane taps are similar enough that the difference in performance is attributable to the position differences between reflections from the ground-based cane tip and the mouth, essentially a head-mounted echo emitter. This raises the possibility that active oral signals may provide cues more useful to precise localization, while ambient sound fields contain enough information for tasks such as shorelining along a solid obstacle. Regardless of the specific cues used, further research evaluating echolocation as a mobility aid should employ classic tasks such as wayfinding, curb detection, doorway detection and passable gap judgments; catalog individual differences in proficiency and utility; and gauge optimal learning approaches.

The perception of objects

Beyond navigation and navigation-based obstacle perception, an important specific strength of active echolocation over passive hearing may lie in the perception of acoustically reflective objects in the environment. In non-human echolocating mammals such as bats and dolphins, echolocation is critical to prey detection, discrimination and tracking (Thomas et al., 2004). In humans, diverse aspects of echoic object perception have been investigated by a variety of studies, many of which are graphically summarized in Figs. 3-1 and 3-2.

Detection

Detecting objects is basic to interacting with the environment. Echolocation studies probing the presence or absence of an object, and the range at which objects of a given size or material can be detected, are abundant in the non-human literature. Bottlenose dolphins have demonstrated threshold distances of over 100 m when detecting 7.62 cm metal spheres, while bats (echolocating in air, a much less acoustically conductive medium) have detected 1.9 cm spheres at distances of just over 5 m (Au, 2004). Detection threshold distances at this scale have not been probed reliably in actively echolocating humans, in part because most experimental setups for non-navigation object perception studies are smaller in scale.

Kohler (1964) tested 267 blindfolded sighted subjects in the detection of a 50 cm cardboard disc, held via a long pole in front of the subject’s face at varying distances. When subjects were silent, two-thirds of them could not detect the disc at all. Fewer than 20 of the remainder reported perceiving the disc at 35 cm or more. When subjects wore an artificial sound generator around the neck, performance increased vastly; all subjects perceived the disc initially, with the best 21 performers reporting perception past 170 cm.

Further research on small-target detection began to establish thresholds and group differences between blind and sighted subjects (Rice, 1967, 1969; Rice et al., 1965). Subjects sat in a special echo-damped chamber while an aperture in the ceiling permitted the presentation, via a thin metal rod, of circular metal discs of varying sizes. The smallest detectable object at each distance was probed via repeated presentations (method of constant stimuli) across sizes and distances; subjects produced their own echo vocalizations before answering “Yes” or “No” to indicate the presence or absence of a target. Remarkably, when expressing thresholds across all distances, a relatively constant quantity emerged: in the range of distances probed (61 to 274 cm), threshold target sizes all subtended a mean angle of about 4.6° (Rice et al., 1965). Interestingly, when early-blind, late-blind and sighted subjects were compared, threshold target sizes were significantly smaller than those of both late-blind and sighted subjects, who did not differ statistically from each other.

In conducting echo-detection experiments with small targets, Rice et al. (1965) did not find a maximum distance for object detection within the bounds of their laboratory equipment. Thus, as with unexplored anecdotal reports of long-distance echolocation described above, the maximum possible spatial bounds of echoic object detection remain undelineated.

Object size perception

Size discrimination

In a now classic report establishing the viability of psychophysical methods applied to echo perception, Kellogg (1962) tested two sighted and two blind participants on several active echolocation tasks, including discriminating the sizes of painted wooden discs at several short distances. At distances of 30.5, 61, and 92 cm, subjects were presented with pairs of discs in sequence one comparison disc against a “standard” size, and judged the size of the comparison disc relative to the standard after making vocalizations of their choice, which included clicks, hisses and spoken words. One blind subject displayed remarkable sensitivity at 30.5 cm that broke down completely at 61 cm; the other blind subject had lower sensitivity at 30.5 cm but did not show the same distance-dependent decrement.

Thus, the ability to discriminate echoically between objects of different sizes was shown, but little else was revealed about the properties of this perceptual ability. Kellogg’s (1962) results are incomplete in several ways. For example, the performance data of only one of two blind subjects was actually reported, the other simply receiving a brief description in the text. In a footnote, the two sighted control subjects were described as having no success, with no data shown. Finally, each of three distance conditions was tested only once, in an unreported order, providing no information about practice effects.

A subsequent size discrimination study (Rice and Feinstein, 1965) tested four blind subjects on a similar task, judging pairs of metal discs in a range of five target sizes. The subjects were well practiced in echolocation tasks and were permitted to make any sound that was their typical vocalization, such as clicks or hisses. Relatively fine thresholds, expressed as area ratios of a larger threshold target compared to a standard, were reported, on the order of approximately 1.1 to 1.2 for all three distances tested. No equivalent comparison with sighted subjects was reported.

A larger sample of blindfolded sighted participants was tested in multiple sessions and several distances (Teng and Whitney, 2011; see Chapter 4). Similar stimuli (plastic discs) and distances (33–75 cm) were used; unlike Kellogg and Rice and Feinstein, each pair of discs was presented simultaneously, allowing subjects to make a near-simultaneous echo comparison. Subjects were instructed to use tongue clicks. As previously reported (Kellogg, 1962), sighted blindfolded participants were initially completely unable to perform the judgments, performing at chance levels and reporting subjective confusion. However, within four 100-trial sessions, robust group thresholds of approximately 17° and 19° angular size difference between stimuli were found for sighted subjects at 33 and 50 cm, respectively.

In summary, object size differences appear to be correlated with an echo signature that is available to listeners and indexes a constant value, whether ratio of areas (Rice and Feinstein,

1965) or difference in subtended angle (Teng and Whitney, 2011). While initially discriminated best by blind listeners, this signature is readily available to a fair degree of precision for sighted persons as well, given a small amount of training. The specific acoustic echo cues underlying size have not been empirically identified, but are likely to be related to a larger surface being available to reflect echo pulses. This would affect the intensity of the echo return, as well as its spectral range, especially at smaller sizes.

Size constancy

Echoic absolute size perception and constancy have not been well researched in humans. As a sound does not have inherent spatial extent when impacting the sensory periphery (as opposed to a visual stimulus stimulating the retina), the cues for this perception are not immediately obvious. Relatedly, however, recent work (Heinrich and Wiegrebe, 2013) has investigated size invariance in echolocating bats. Using a virtual echo setup, the angular size (sonar aperture) and distance of virtual echoic objects was manipulated, and the bats were trained to choose the larger object. Given that successful interaction with the external environment must demand some perceptual constancies for objects, it is perhaps surprising that the bats consistently chose the wider auditory angle, regardless of virtual distance, rather than adjusting perceived size for distance. A control experiment verified that the distance information *per se* was well above the bats' discrimination thresholds. Thus, Heinrich and Wiegrebe (2013) speculate that size constancy in echolocation may simply not be necessary, especially given that bats can still use vision for size judgments.

Blind human echolocators do not have vision available to perform these judgments. Thus it remains possible that they do use some echolocation-based mechanisms to maintain stable representations of object size. This might consist of echoic absolute distance estimates; other factors, such as self-motion or haptic and somatosensory cues, may contribute to the perceived size of echoic objects.

Localization

Localization of objects is among the most important features of perception. Echolocation experiments testing spatial resolution, i.e. the accuracy of localization, have largely focused on judgments of absolute position along the horizontal plane. Perhaps the classic study of echoic absolute position judgments was conducted by Rice (1967, 1969). Three groups of subjects — early-blind, late-blind and sighted — sat at the center of an apparatus that positioned a disc at random 15° increments along a 180° horizontal semicircular arc in the frontal plane. On each trial, subjects would make echolocation vocalizations while facing straight ahead, then indicate the perceived position of the disc by turning their heads to face it. Localization accuracy by all groups was good and very similar inside 15° from the mid-sagittal plane. Starting at 30°, late-blind subjects began to display increasing errors in the form of mislocalizations and detection failures. Sighted subjects fared worse, unable even to detect the targets past 60° azimuth. Rice (1969) concluded that echolocalization performance, especially in the periphery, appeared to benefit from blindness, early-onset blindness in particular.

Several studies have employed laterality judgments, in which a two-alternative forced-choice (2AFC) judgment is made regarding whether an object is to the right or left or the subject's mid-sagittal plane (Despres et al., 2005; Dufour et al., 2005; Rowan et al., 2013; Thaler et al., 2011). Dufour et al. (2005) and Despres et al. (2005) found that in judging echoes generated by pulses from a speaker at the subject's position, blind subjects performed more accurately than the normally sighted in correctly identifying the lateral position of a reflecting surface. However, they were also more susceptible to bias from spurious echo cues, indicating an overall greater sensitivity to echoes compared to sighted subjects, rather than a unilaterally superior cognitive strategy (Dufour et al., 2005). Remarkably, this relationship was not only true for blind versus sighted subjects but also for myopic versus normal-sighted subjects (Despres et al., 2005).

The lateral position paradigm of Dufour et al. (2005) was adopted for further acoustic and psychophysical investigation of the cues available for making lateral position judgments (Papadopoulos et al., 2011; Rowan et al., 2013). Using virtual echoes presented to subjects via headphones, the authors found that given appropriate stimulus properties, subjects could reliably judge the lateral position of a board positioned to either side of the median plane. When the board was angled such that its surface normal pointed directly to the subject, performance improved and was less susceptible to increasing distance, remaining high even at nearly 2 m distance, when it had dropped to chance levels for the flat board (Rowan et al., 2013). Based on modeling and acoustic analyses, the authors concluded that specular reflection paths strongly affected the localization cues available to listeners. This cue-based analysis was supported by the fact that blind and sighted subjects performed equally poorly when the distance increased such that the reflection path no longer returned information to the listener. At lower distances, six blind subjects tended to perform slightly better than 13 sighted subjects, though quantitative comparison was hampered by the small sample size of blind subjects.

In establishing the spatial acuity of echolocation judgments in two expert echolocators, Thaler et al. (2011) reported a localization precision of 3° and 9° of azimuth for a concave reflecting half-cylinder ensonified by an early- and late-blind subject, respectively. The subjects performed almost equivalently on a passive-listening task using the same recorded echo stimuli.

Relative rather than absolute position judgments are also important to spatial perception. In vision, for example, fine-scale relative position information can be probed using a vernier offset task, in which two visual stimuli (typically lines or dots) are offset orthogonal to their axis of alignment. Importantly, vernier judgments have yielded hyperacuity, the finest visual resolution ever measured. Thus, we set out to measure the spatial resolution of echolocation using an auditory analogue to this task (Teng et al., 2012; Teng and Whitney, 2011). Plastic discs mounted on a wooden frame were aligned vertically and set off by various center-to-center horizontal distances. Subjects were told to echolocate the frame using tongue clicks and judge whether the top disc was to the left or right of the bottom disc. We found that some sighted subjects could perform this task, but that it was extremely difficult, with very large individual differences among subjects (Teng and Whitney, 2011). By contrast, a sample of six blind expert echolocators, who reported using echolocation as an everyday mobility and perceptual aid, performed robustly on the task, discriminating separations subtending angles as fine as 1.2° at a distance of 1 m (Teng et al., 2012). These thresholds currently represent the finest spatial acuity reported for echolocators to date. While the sample was small, results additionally revealed that the age of blindness onset was a strong predictor of precision, suggesting a role for something akin to a critical period for blindness to affect echolocation abilities. However, the relative contributions of age of blindness, duration of blindess, and practice effects remain to be fully described.

In sum, the spatial resolution of echolocation can be quite fine-grained. While not at the level of typical foveal visual acuity, spatial thresholds can be surprisingly fine, in some cases approaching the acuity limits of the human auditory system performing passive hearing tasks. These fine resolutions in expert echolocators have rivaled that of vision in the periphery. Consistent evidence across studies also indicates that blind persons outperform the sighted on these tasks, early-blind subjects especially so. This suggests a crucial role for blindness in echolocation, likely in the form of spurring a functional reorganization of sensory processing; this evidence is in line with prior and concurrent work indicating behavioral advantages in passive hearing tasks in blind compared to sighted subjects (Gougoux et al., 2005; Lessard et al., 1998; Röder et al., 1999).

Target range

Most echolocalization studies have focused on azimuthal localization, possibly following an emphasis on the horizontal axis in the passive spatial hearing literature. Fewer studies have addressed the radial third dimension, for which, informationally, echolocation is extremely well suited. Fine distance discrimination judgments on the order of 1 cm and finer have been amply demonstrated in non-human echolocating animals (Au, 2004). However, target range has been explicitly probed less often than it has been manipulated in the investigation of other variables such as detection or localization. The "final appraisal" judgments of the Cornell and similar studies may qualify as a distance judgment of sorts, but no estimates of absolute distance, nor explicit distance comparisons were asked of the subjects; they simply walked to positions they believed to be either closely near (Ammons et al., 1953; Cotzin and Dallenbach, 1950; Supa et al., 1944) or directly at (Rosenblum et al., 2000) the position of the obstacle they were trying to perceive.

Kellogg (1962) found that two blind subjects could judge differences in the distance of a 30 cm wooden reflecting disc at 60cm, with thresholds as fine as 11 cm. Two sighted subjects were completely unable to do so. Curiously, it is not clear whether the subjects were consciously performing a distance judgment: a disc that was closer appeared "larger" and vice versa; behavioral responses appear to be reported in terms of size judgments for this task.

More recently, an investigation of echoic target range discrimination (Schörnich et al., 2012) used a sophisticated virtual echo setup in which subjects produced echo clicks, which were picked up by a microphone and rapidly processed and played back to simulate echo-reflecting surfaces at various distances. Subjects thus performed a 2AFC discrimination task testing sensitivity to distance variations at ranges of 1.7, 3.4 and 6.8 m. Typical threshold differences were below 1 m, and below 50 cm at a 1.7 m range. Notably, these Weber fraction in the range of .1-.2 for sighted subjects compare well with the fractions of .18 and .30 measured by Kellogg (1962).

Object discrimination and identification

Highly sophisticated object-level perception has been documented in bats identifying prey (Thomas et al., 2004) and dolphins integrating object information (Harley et al., 2003) across sensory modalities. This level of object perception, in which the relevant cues are likely to be considerably more complex than for detection or localization tasks, has only been scantily characterized in humans.

Texture

Echoic discrimination between different textures, such as wood, metal, and fabric, has been shown in both blind (Kellogg, 1962) and sighted (Hausfeld et al., 1982) participants. Kellogg's (1962) blind subjects were readily able to distinguish between hard (e.g., wood, metal) and soft (fabric, velvet) surfaces. Discrimination among hard or soft surfaces proved more difficult. Subjects in Hausfeld et al.'s (1982) study identified, rather than discriminated, various surfaces presented to them; among four possible surfaces, performance was above chance for fabric and wood.

Shape

Hausfeld et al. (1982) also tested two-dimensional echoic shape perception in sighted subjects, with above-chance identification of squares, circles and triangles by sighted subjects who were encouraged to move their heads laterally in a "scanning" motion to ascertain the shape features. More recent studies have distinguished between flat and concave shapes, which bear the added advantage of differentially focusing an echo return and thus providing a cue that can be accessed without head movements. Expert echolocators were able to distinguish flat from concave shapes, though performance was above chance in one study (Thaler et al., 2011) and not different from chance in another (Arnott et al., 2013). No sighted subject was able to perform above chance levels.

Echo perception of object-level features such as shape and texture, even high-level holistic object information, remains poorly characterized, but echo returns from complex surfaces do appear to contain enough information for discrimination.

Summary and motivation

The outlines of behavioral performance in human echolocation presented here are fairly general. Among the more pervasive questions that persist in echolocation research are: (i) whether the skill is unique to blind persons (cf., e.g., Rice, 1969) or available to any person with training and adequate hearing; and (ii) how far the limits, e.g. acuities, of echolocation reach. Despite some previous research (Ammons et al., 1953; Kohler, 1964; Rice and Feinstein, 1965; Rice et al., 1965), active echolocation has been tested only cursorily in this context until recently. Thus, in the following chapters I present two studies addressing the question of learning echolocation tasks by sighted listeners, a subject group traditionally underrepresented in the field; and an investigation of fine-grained spatial acuity in an echolocalization task performed by blind echolocation experts.

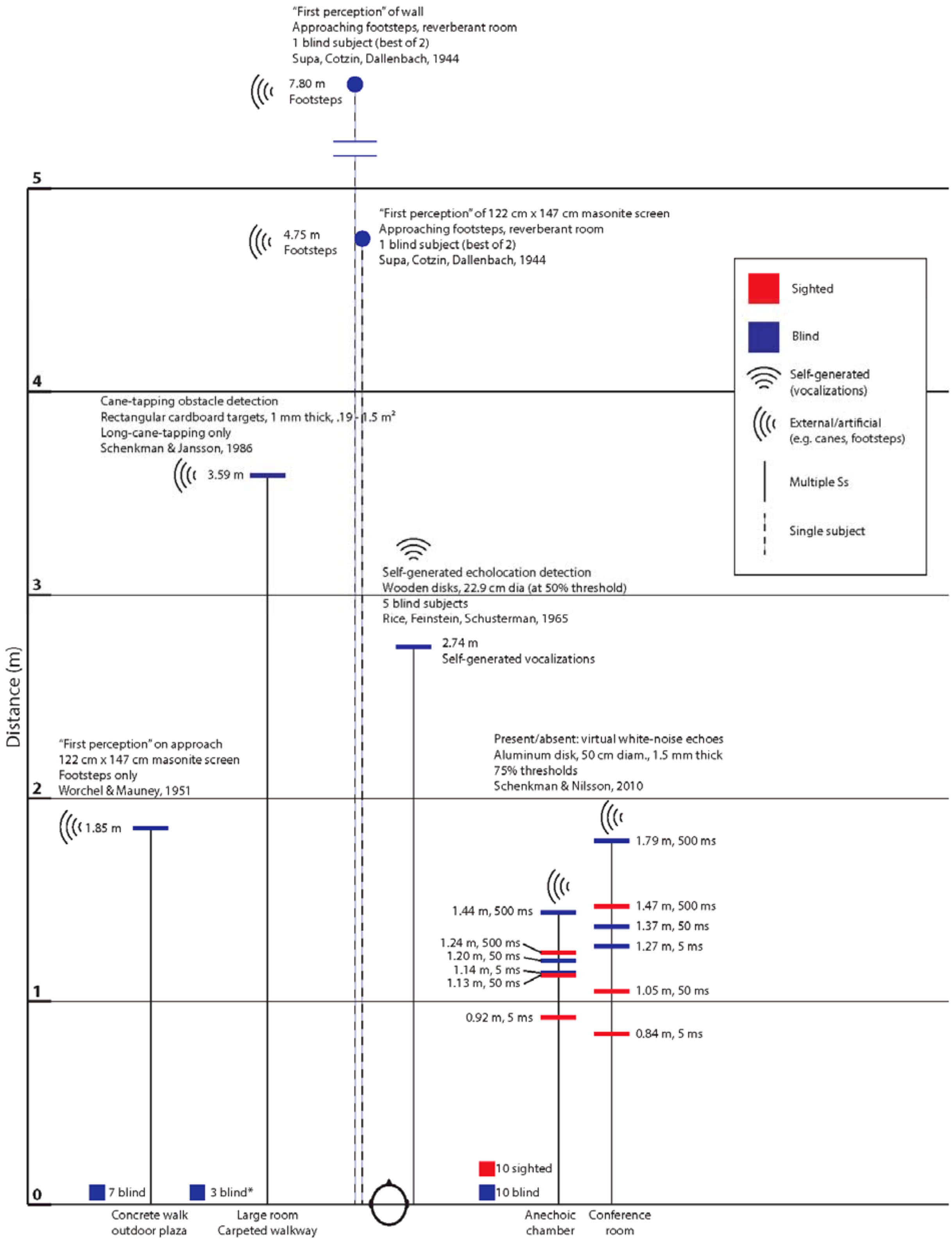

"First perception" of wall
Approaching footsteps, reverberant room
1 blind subject (best of 2)
Supa, Cotzin, Dallenbach, 1944
7.80 m
Footsteps
5
"First perception" of 122 cm x 147 cm masonite screen
Approaching footsteps, reverberant room
1 blind subject (best of 2)
Supa, Cotzin, Dallenbach, 1944
4.75 m
Footsteps
Sighted
Blind
Self-generated (vocalizations)
External/artificial (e.g. canes, footsteps)
Multiple Ss
Single subject
4
Cane-tapping obstacle detection
Rectangular cardboard targets, 1 mm thick, .19 - 1.5 m²
Long-cane-tapping only
Schenkman & Jansson, 1986
3.59 m
Self-generated echolocation detection
Wooden disks, 22.9 cm dia (at 50% threshold)
5 blind subjects
Rice, Feinstein, Schusterman, 1965
3
2.74 m
Self-generated vocalizations
Distance (m)
"First perception" on approach
122 cm x 147 cm masonite screen
Footsteps only
Worchel & Mauney, 1951
2
Present/absent: virtual white-noise echoes
Aluminum disk, 50 cm diam., 1.5 mm thick
75% thresholds
Schenkman & Nilsson, 2010
1.85 m
1.79 m, 500 ms
1.47 m, 500 ms
1.44 m, 500 ms
1.37 m, 50 ms
1.27 m, 5 ms
1.24 m, 500 ms
1.20 m, 50 ms
1.14 m, 5 ms
1.13 m, 50 ms
1
1.05 m, 50 ms
0.92 m, 5 ms
0.84 m, 5 ms
10 sighted
10 blind
0
7 blind
3 blind*
Concrete walk
outdoor plaza
Large room
Carpeted walkway
Anechoic
chamber
Conference
room

Figure 3-1

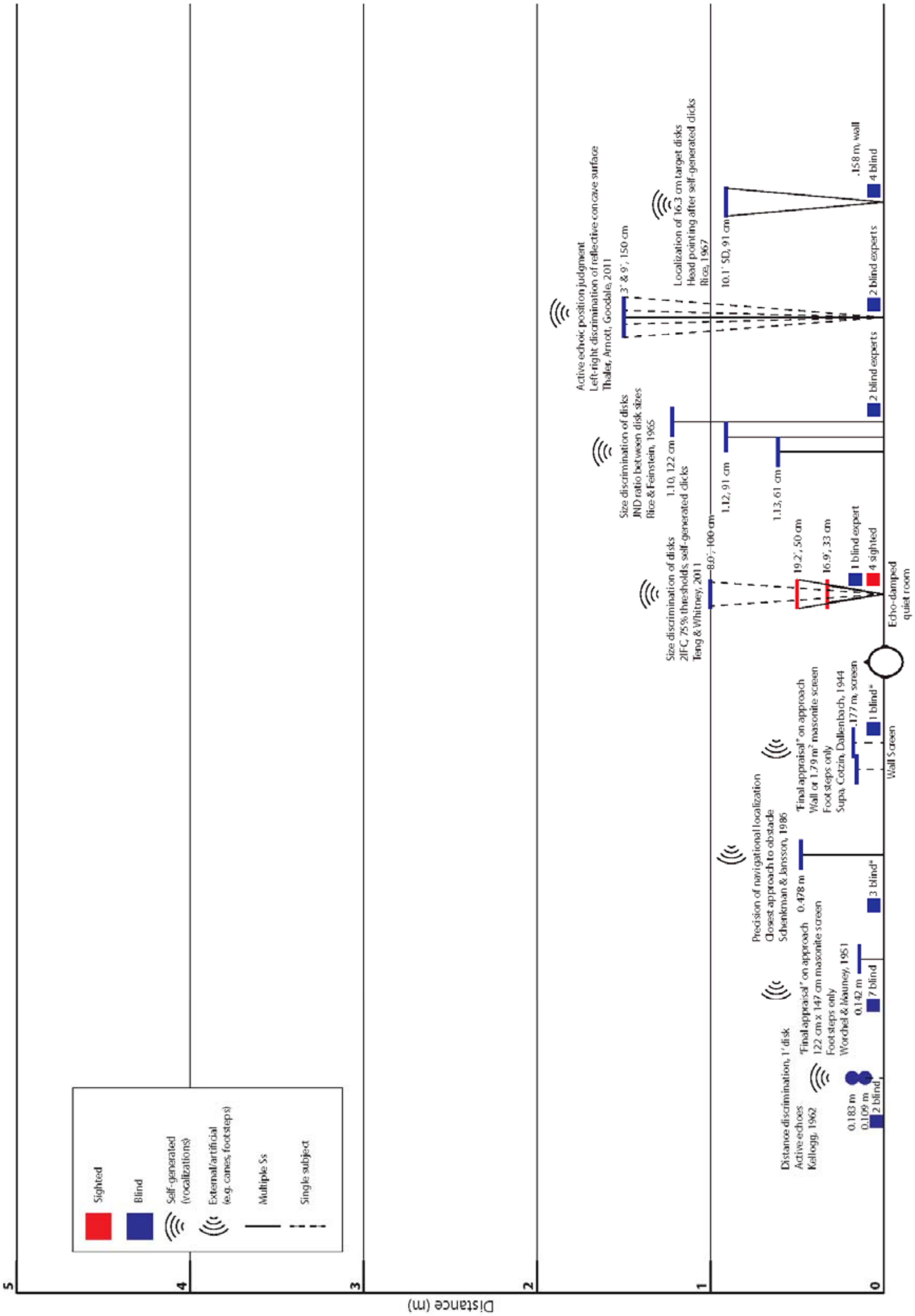

Distance (m)
0
1
2
3
4
5
Sighted
Blind
Self-generated (vocalizations)
External/artificial (e.g. canes, footsteps)
Multiple Ss
Single subject
Distance discrimination, 1' disk
Active echoes
Kellogg, 1962
0.183 m
0.109 m
2 blind
"Final appraisal" on approach
122 cm x 147 cm masonite screen
Foot steps only
Worchel & Mauney, 1951
0.142 m
7 blind
Precision of navigational localization
Closest approach to obstacle
Schenkman & Jansson, 1986
0.478 m
3 blind*
"Final appraisal" on approach
Wall or 1.79 m² masonite screen
Foot steps only
Supa, Cotzin, Dallenbach, 1944
.177 m, screen
1 blind*
Wall Screen
Echo-damped quiet room
Size discrimination of disks
2IFC, 75% thresholds, self-generated clicks
Teng & Whitney, 2011
8.0°, 100 cm
19.2°, 50 cm
16.9°, 33 cm
1 blind expert
4 sighted
Size discrimination of disks
JND ratio between disk sizes
Rice & Feinstein, 1965
1.10, 122 cm
1.12, 91 cm
1.13, 61 cm
2 blind experts
Active echoic position judgment
Left-right discrimination of reflective concave surface
Thaler, Arnott, Goodale, 2011
3° & 9°, 150 cm
2 blind experts
Localization of 16.3 cm target disks
Head pointing after self-generated clicks
Rice, 1967
10.1° SD, 91 cm
.158 m, wall
4 blind

Figure 3-2

(Preceding pages)

Figure 3-1. A spatially organized overview of echolocation detection results. Mean detection distances (y-axis) are indicated by vertical lines capped by circles and dashed lines for single-subject results and horizontal lines and solid lines for multi-subject results. Blue bars indicate blind subjects; red indicates sighted. For scale, an average-sized head is shown on the x-axis.

Figure 3-2. A spatially organized overview of echolocation localization results. Mean thresholds are indicated by vertical lines capped by circles and dashed lines for single-subject results and horizontal lines and solid lines for multi-subject results. Angular resolution is indicated by appropriate angles extending out to the distance at which judgment was made. Blue bars indicate blind subjects; red indicates sighted. For scale, an average-sized head is shown on the x-axis. For comparison, the y-axis scale is kept identical to that in Fig. 3-1.

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

Abstract

Sighted novices' echolocation performance was compared with that of a blind expert, revealing rapid learning of size and position discrimination with surprising precision. Using a novel task, we characterize the population distribution of echolocation skill in the sighted and report the highest known human echolocation acuity in our expert subject.

Introduction

Echolocation is a specialized application of spatial hearing in which objects are localized and the external environment represented with the aid of reflected auditory information. Among non-human species, it has been documented and studied extensively, particularly in microchiropteran bats and odontocete cetaceans (Au and Benoit-Bird, 2003; DeLong et al., 2006; Harley et al., 2003; Simmons et al., 1992; Teeling et al., 2000; Thomas et al., 2004). Echolocation functions in these species are thought to include navigation and orienting, hunting, and social communication.

Although it is currently an uncommon practice, there are some blind humans who actively use echolocation for pragmatic reasons. Humans do not possess the highly specialized neural systems of bats and marine mammals for target rangefinding or velocity determination. Still, the purpose of echolocation for these individuals, and for future practitioners, might include navigation and goal-directed action, object recognition, and texture perception. The basis of all of these functions lies in the spatial resolution of the ability, as outlined by the conceptual framework we propose in Figure 4-1. Without sufficient spatial resolution, recognizing objects, surfaces, and scenes, as well as navigation, becomes difficult or impossible. The principle is similar to that articulated for visual processing by Marr (Marr, 1982) and summarized for auditory models by Slaney (Slaney, 1998).

Reports dating back several centuries describe a capacity for object perception in some blind individuals, though for most of that time even the most general mechanism of this so-called "obstacle sense" or "facial vision" was unknown (cf. Supa et al., 1944). Modern, albeit largely qualitative, experimental studies of human echolocation began in the 1940s and continued with increasing psychophysical rigor for roughly two decades (Ammons et al., 1953; Cotzin and Dallenbach, 1950; Kellogg, 1962; McCarty and Worchel, 1954; Rice and Feinstein, 1965; Supa et al., 1944; Worchel and Dallenbach, 1947). A great deal became known about this ability during that period, beginning with the unequivocal determination of its auditory nature. In blind individuals, echolocation has been found useful for determining the presence or absence, size and distance, and material and shape properties of objects and obstacles.

However, the question of the extent to which echolocation abilities are accessible to *sighted* subjects has received far less attention. Beyond simple existence proofs, the echolocation performance of sighted people remains a largely open question, as research has been sparse and nonsystematic. Some studies of related perceptual skills, such as passive echo perception and auditory spatial localization, have reported the ability of sighted subjects to echo-detect stimuli and discriminate gross differences in some shapes and textures (Hausfeld et al., 1982; Rice, 1969), although the skills of the sighted subjects were consistently and considerably worse than the blind subjects. Kellogg's blindfolded sighted subjects (1962) showed virtually no ability to discriminate the sizes, distances or textures of stimuli presented to them. More recent investigations have tested sighted subjects using externally (Despres et al., 2005; Dufour et al., 2005; Hughes, 2001) and self-generated (Rosenblum et al., 2000) echoes. However, the echolocation tasks in those studies either tested only coarse lateralization (Despres et al., 2005; Dufour et al., 2005), measured spatial judgments without individual precision measurements in a navigational context (Hughes, 2001), or tested auditory looming in locomotion (Rosenblum et al., 2000). 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 also note that the literature is sorely lacking in this regard, especially for sighted subjects.

Tables 4-1a and 4-1b give an overview of prior echolocation studies in which blind and sighted humans were involved. Table 4-1a includes psychophysical echolocation experiments involving self-generated echo stimuli. Table 4-1b includes the remainder of human echolocation studies. It is apparent from inspecting the studies that very few psychophysical experiments with sighted subjects have actually been conducted, especially when considering only those 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, and they present conflicting results, with Kellogg's subjects being unable to perform the task and Rice's subjects performing 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, none more so than the Snellen chart (Snellen, 1863). Other, more powerful measures of the spatial resolution of vision are also available (Kniestedt and Stamper, 2003). Because human echolocation is often discussed as an auditory perceptual aid in navigation and object perception, it is appropriate to quantitatively investigate not only detection thresholds, but the limits of the spatial acuity this ability affords its practitioners. The beginnings of such quantifications have been described in blind subjects (Rice and Feinstein, 1965; Rice et al., 1965); but almost nothing is known of similar characteristics in the sighted (and, therefore, newly blind). Thus, the goal of this study is to characterize quantitatively the spatial precision with which sighted subjects can echolocate. In addition, we will directly compare the spatial resolution of echolocation in sighted novices with that of a blind expert echolocator. Our results from two experiments will show that some sighted individuals can learn to echolocate with extraordinary precision, approaching that of early blind experts.

Experiment 1: Size discrimination

The goal of the first experiment was to measure echolocation and learning of echolocation in sighted subjects performing a size discrimination task. As similar size discrimination tasks have been used before (Hausfeld et al., 1982; Kellogg, 1962; Rice, 1969), with mixed results, it is appropriate to use a size discrimination paradigm for purposes of comparison to previous studies.

Methods

We conducted the size discrimination experiment in a soundproof, echo-damped room. Eight healthy, neurologically normal subjects participated in the experiment. Participants were blindfolded and seated 33 cm from a frame supporting two flat, circular plastic acrylic discs painted with primer to give them a uniform, matte reflecting surface. The largest disc (diameter 25.4 cm) served as the standard stimulus and was randomly located on the top or bottom of the display. One of the other six comparison disks, ranging from 5.1 to 22.9 cm in diameter, was located in the other spatial position (bottom or top, respectively). The independent measure of interest was the auditory angle (measured from the ears) subtended by the difference between the standard and comparison disk diameters in each pairing condition (Fig. 4-2). These auditory angle differences ranged from 4.4° to 31.7°.

Subjects performed a 2AFC task using the method of constant stimuli in which they were asked to judge whether the larger stimulus was on the top or bottom of the display. The task was performed two times sequentially in each trial. The first, passive judgment (the "preclick" judgment) served to control for any ambient auditory information that may have been present in the sound-proofed room. The beginning of the trial was signaled by the experimenter via a knock on the table or tap on the shoulder. Thresholds remained unaffected by this procedure (see Fig. 4-3a). For the second, "postclick" judgment, subjects used active echolocation: they made clicking noises with their tongues against the roofs of their mouths and made the judgment at their own pace. Importantly, no feedback was given to subjects after either judgment or at any other time during this experiment.

Participants were allowed to pitch their heads vertically and make as many clicks as they felt were necessary to allow a judgment. They were not allowed to swivel their heads from side to side, translate their heads in any direction, or produce sounds other than clicks. Each session contained 100 trials and lasted between 1 and 2 hours. Each subject underwent four sessions.

To investigate the effects of manipulating distance from the stimuli, we conducted additional sessions at 33, 50 and 75 cm for a subset of four subjects after they had completed the initial four-session training period. The auditory angle differences in the more distant 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 the services of DK, an echolocator who has been totally blind since early infancy, taught himself to echolocate during childhood, and now operates a school to teach echolocation to blind and sighted individuals. DK was not available for the length of time required for an extended battery of psychophysical sessions. However, given that he has accumulated three decades' worth of echolocation practice, we felt that even a single session could serve as a reasonable benchmark of expert performance, even in a novel task. To avoid ceiling effects, we tested DK at a distance of 75 cm, where angular differences between stimuli subtended from 1.9° to 15.0°.

Analysis

Performance data from the sessions at 33 cm were analyzed in two ways. First, we tested the hypotheses that larger differences between stimuli made judgments easier, that clicking provided an advantage in subjects' psychophysical judgments, and that performance would improve with training. To do this, we conducted a three-way (4x2x6) repeated-measures ANOVA with within-subject factors of Session, Clicking (pre- vs. post) and Separation. Subsequent post-hoc ANOVAs were performed to further elucidate interactions between Session and Clicking (see RESULTS).

Second, when subjects performed well enough to calculate a 75% threshold (i.e., performance exceeded 75% correct at the easiest condition), we fitted psychometric curves (Equation 4-1a) to results from individual runs as well as group data. The curve fitting utilized the maximum-likelihood method described by Wichmann and Hill (Wichmann and Hill, 2001a) and implemented in the psignifit toolbox for Matlab 7.1 (The Mathworks, Natick, MA). The psychometric data were fit with a logistic function (Equation 4-1b).

$$\Psi(x) = \gamma + (1 - \gamma - \lambda) \cdot F(x, \alpha, \beta) \quad \text{(4-1a)}$$

Where

$$F(x,\alpha,\beta) = \frac{1}{1 + e^{-\frac{x-\alpha}{\beta}}} \quad \text{(4-1b)}$$

The baseline performance parameter, γ, was always set to 0.5, and the asymptote offset parameter, λ, was fixed at 0 (i.e., maximum performance was set to 100%). Parameter α is the discrimination threshold, and parameter β is the slope of the psychometric function. Confidence intervals were generated based on 10,000 simulations using psignifit's BC_a bootstrapping method (Wichmann and Hill, 2001b) (see Fig. 4-3a for a single-session example). Monte Carlo simulation, implemented in psignifit's pfcmp subfunctions, was used to make pairwise comparisons between psychometric functions. 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 4-3a shows pre- and postclick data for sighted subjects' first four sessions at a distance of 33 cm. The solid lines represent performance in the clicking condition, while dashed lines represent the preclick baseline. A three-way (4x2x6) repeated-measures ANOVA with within-subjects factors of Session, Clicking (pre- vs. post) 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 x Clicking interaction ($F_{3,21}$=4.75; p=.011) suggests that session effects were carried by the postclick condition, while preclick baseline performance remained stable. Subsequent repeated-measures ANOVAs performed separately on the pre- and postclick conditions confirmed this, showing a significant main effect of Session ($F_{3,21}$=3.59; p=.031) for the postclick condition, but not for preclick ($F_{3,21}$=2.48, p=.09). Preclick data collapsed over all 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 all subjects underwent 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 4-3b emphasizes session effects in terms of difference scores between pre- and postclick performance rather than raw percentages.

Representative psychometric functions for one skilled sighted observer, BL, and blind expert echolocator DK are shown in Fig. 4-3c. Their 75% thresholds (14.5° and 8.0°, respectively) indicate that both subjects 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 DK's single-session threshold).

Figure 4-4 shows pooled postclick data from the four observers who underwent additional sessions at larger distances. For comparison, data from DK's single size-discrimination session is shown as well. Each of the three group curves represents the averaging of three sessions for each of four observers at the distance indicated. To ensure the averaging of asymptotic performance data from the sighted subjects, the last three sessions at each distance were used. Repeated-measures ANOVAs (3x2x6, Session x Clicking x Separation) performed on data at each distance confirmed this, showing no significant main effects of Session at any distance (all $F_{2,6}$ < .80; p > .49). Regardless of the distance, performance appeared to vary along the same curve when plotted against the angular size difference, independently of linear distance. Psychometric curves fitted to group performance at 33 and 50 cm (the two distances for which mean subject performance exceeded 75%) yielded similar thresholds: 16.9° for 33 cm and 19.2° for 50 cm. 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 is achieved by sighted observers 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 an expert blind echolocator, we measured echolocation in an auditory version of a vernier acuity task, similar to that used by vision scientists for decades (Goldstone, 1998; Levi et al., 1985; McKee and Westheimer, 1978). In visual psychophysics, a typical vernier acuity task involves a pair of line segments arranged end-to-end, slightly displaced in a direction orthogonal to their orientation; the participant's instructions are to determine the direction of displacement on each trial (McKee and Westheimer, 1978; Westheimer and McKee, 1977). A distinguishing feature of vernier acuity (as opposed to other measures, like Snellen acuity) is that the comparison judgments between the two lines can give rise to extremely fine discrimination thresholds, smaller than the width of a single photoreceptor (Westheimer, 1979; Westheimer and McKee, 1977). Vernier acuity, therefore, has the power to reveal 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. The adaptation of vernier stimuli to an echo-perception domain affords us a new measure of spatial precision in echolocation performance, uniquely allowing us to measure relative (rather than absolute or egocentric) spatial localization. Spatial perception depends largely on relative localization, and this vernier method therefore provides a means of characterizing the resolution of auditory spatial acuity.

Methods

To measure auditory vernier acuity, we used a setup similar to that used in Experiment 1 (Fig. 4-5a). Sighted participants (N=11) sat blindfolded facing the frame at a distance of 50 cm. Two vertically separated white plastic disks, both 20.3 cm in diameter, were placed on the crossbars, with their centers separated by one of five horizontal distances that subtended from 1.1° to 13.2° of auditory angle (Fig. 4-5a). 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. 4-2c and Experiment 1 Methods). Each observer participated in a minimum of 5 sessions to ensure reaching asymptotic performance.

Expert echolocator DK was available for two sessions of the vernier acuity task. Based on a running average (bin width, 10 trials), DK reached asymptotic performance in the second session. The first session was conducted at 75 cm and the second session at 100 cm, to avoid ceiling effects. In the first session, DK 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°.

As before, participants were allowed to tilt their heads vertically but not swivel horizontally or otherwise move while clicking; distance and orientation were checked periodically during each session by the experimenter. Subjects were given feedback after each trial that indicated both the actual separation between stimuli as well as whether the last response was correct. Because we were interested in absolute thresholds rather than the characterization of a learning curve, we felt that it was appropriate to administer feedback, which has been shown to speed improvement in a vernier task (Herzog and Fahle, 1997). Control sessions conducted with six subjects indicated that neither the absence of feedback nor a relaxation of head-movement restrictions elicited significant changes in thresholds.

Results, Experiment 2

A two-way repeated-measures ANOVA (Clicking x 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 pre- and postclick conditions did not reach significance ($F_{4,40}$=1,98; *p*=.116), the condition x separation interaction was significant ($F_{4,40}$=2.74; *p*=.042). This suggests again that clicking was significantly helpful to subjects, as preclick group performance never exceeded chance levels, and that the effect of stimulus separation is clearly carried by the postclick condition. A repeated-measures ANOVA on only the postclick 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 (Bauer et al., 1998; Westfall and 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. 4-5d).

The representative plots in Fig. 4-5b show psychometric functions fitted to individuals' data using the psignifit toolbox. The task was clearly much more difficult than in Experiment 1; the initial group analysis belies widely varying performance across subjects and sessions (Fig. 4-5c). 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%. This indicates that some subjects were highly proficient at the task, others less so, and some were completely unable to do it. We examined individual subjects' performance more closely and found that two sighted subjects, BL and KK, were the best and most consistent performers of the task in the range of auditory angles sampled by our stimuli. Specifically, they were the only sighted subjects to perform at above 75% correct, allowing for the computation of 75% thresholds from psychometric functions as in Experiment 1. The asymptote offset parameter, λ, was fixed to 0 for the computation of thresholds for BL, KK, and expert subject DK; that is, ceiling performance was set at 100%. Thresholds pooled over all sessions were 4.1° for BL and 6.7° for KK. These are the finest discriminations among sighted subjects in our sample, though not necessarily at an expert level: by comparison, DK'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 was available for the present study, our results suggest that not all sighted subjects can be equally trained to the level of performance seen in BL and KK. Nevertheless, the results convincingly demonstrate sufficiency—it is possible for some sighted subjects to 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, while constraining the vocalizations used to produce echoes to self-generated clicks. The first experiment revealed that coarse echolocation ability could be readily trained in sighted subjects, even without explicit feedback about performance, and that feedback did not significantly alter performance. Further, size discrimination thresholds were roughly constant with increasing distance, suggesting that angular size difference, rather than distance, may be the key metric of size discrimination using echolocation (Rice et al., 1965). The second experiment employed a novel and challenging vernier acuity task to precisely measure the spatial resolution of echolocation. Importantly, in contrast to previous studies (Dufour et al., 2005; Kellogg, 1962), we found that with sufficient training some sighted subjects can learn to echolocate with a level of proficiency that approached that of an early-blind expert echolocator.

In the second experiment, we introduced a new measure of echolocation acuity — the vernier stimulus. The advantage of this stimulus is that it provides a means of operationally defining the acuity of echolocation, akin to the spatial acuity of vision, and could provide 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 DK and BL relative to their size-discrimination performance also suggests that while auditory vernier discrimination may be a more difficult task, it also carries the potential to measure very fine spatial resolution in echolocation.

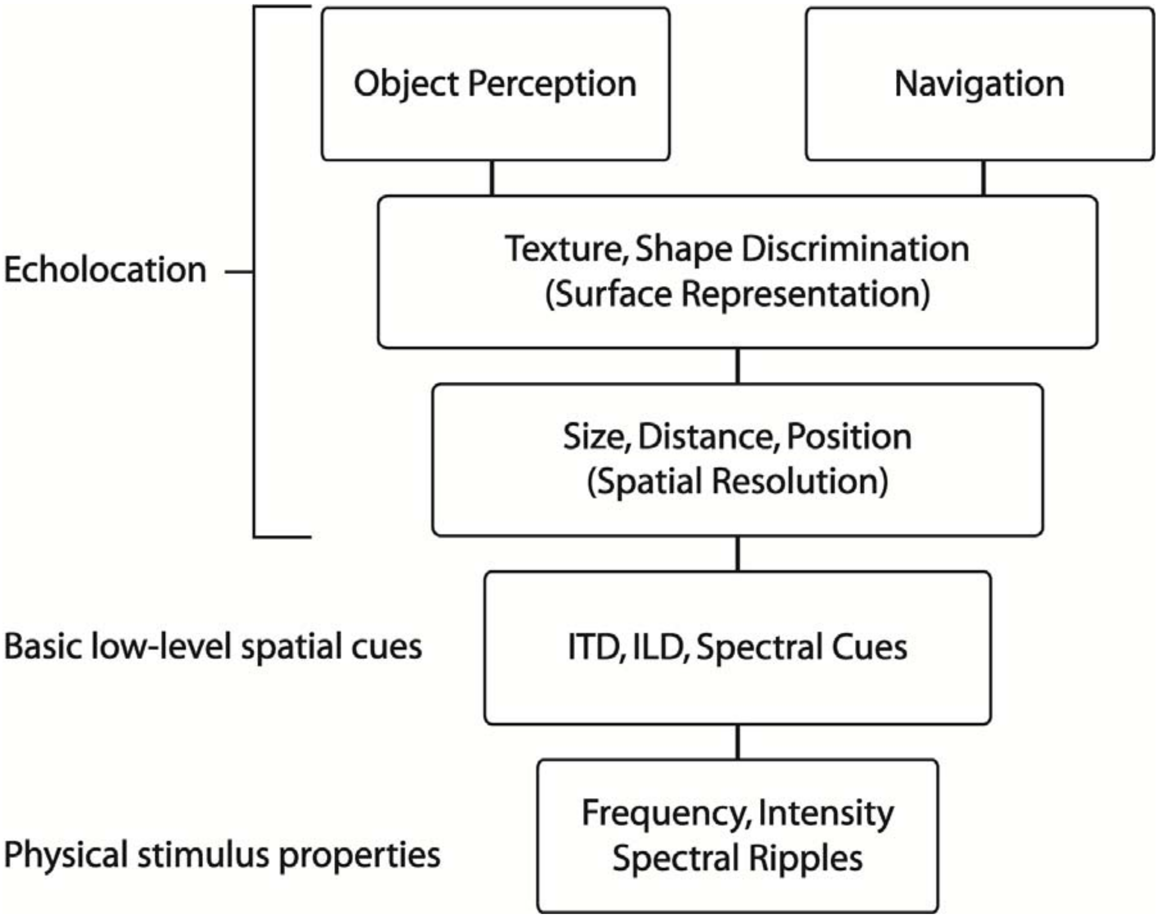


Figure 4-1. Proposed representational framework for various levels of cues served by echolocation. Low-level cues such as sound intensity, timing and frequency produce interaural level difference (ILD), interaural timing difference (ITD) and spectral cues; these are analyzed to perform the basic functions subserved by spatial hearing, such as orientation and detection or discrimination at fine scales. These, in turn, give rise to high-level functions 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.

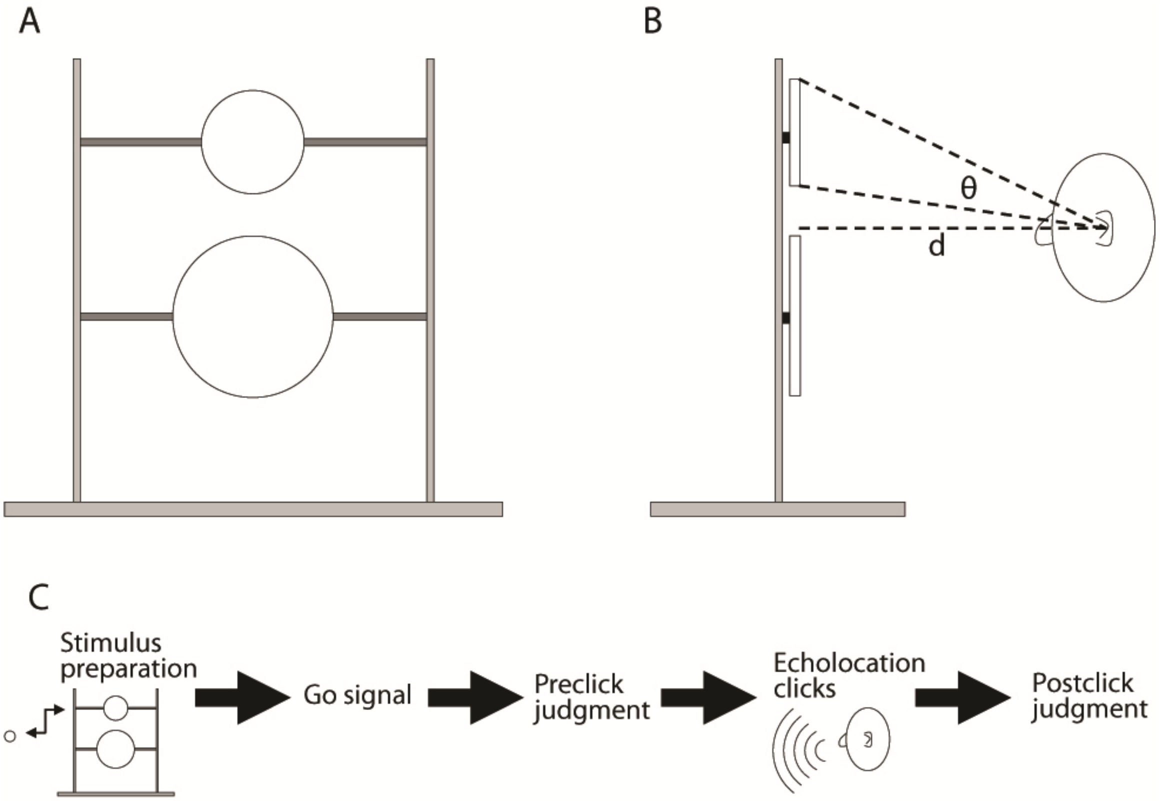


Figure 4-2. Front (A) and lateral (B) views of the echolocation stimulus setup. Subjects sat at distance *d* (33, 50 or 75 cm) from the vertical plane formed by the stimuli, such that stimuli subtended auditory angle θ. Auditory angle differences between stimulus diameters were computed using the distance *d* from the stimulus plane. Trial sequence, including control and active echolocation judgments, is shown in Fig. 4-2C.

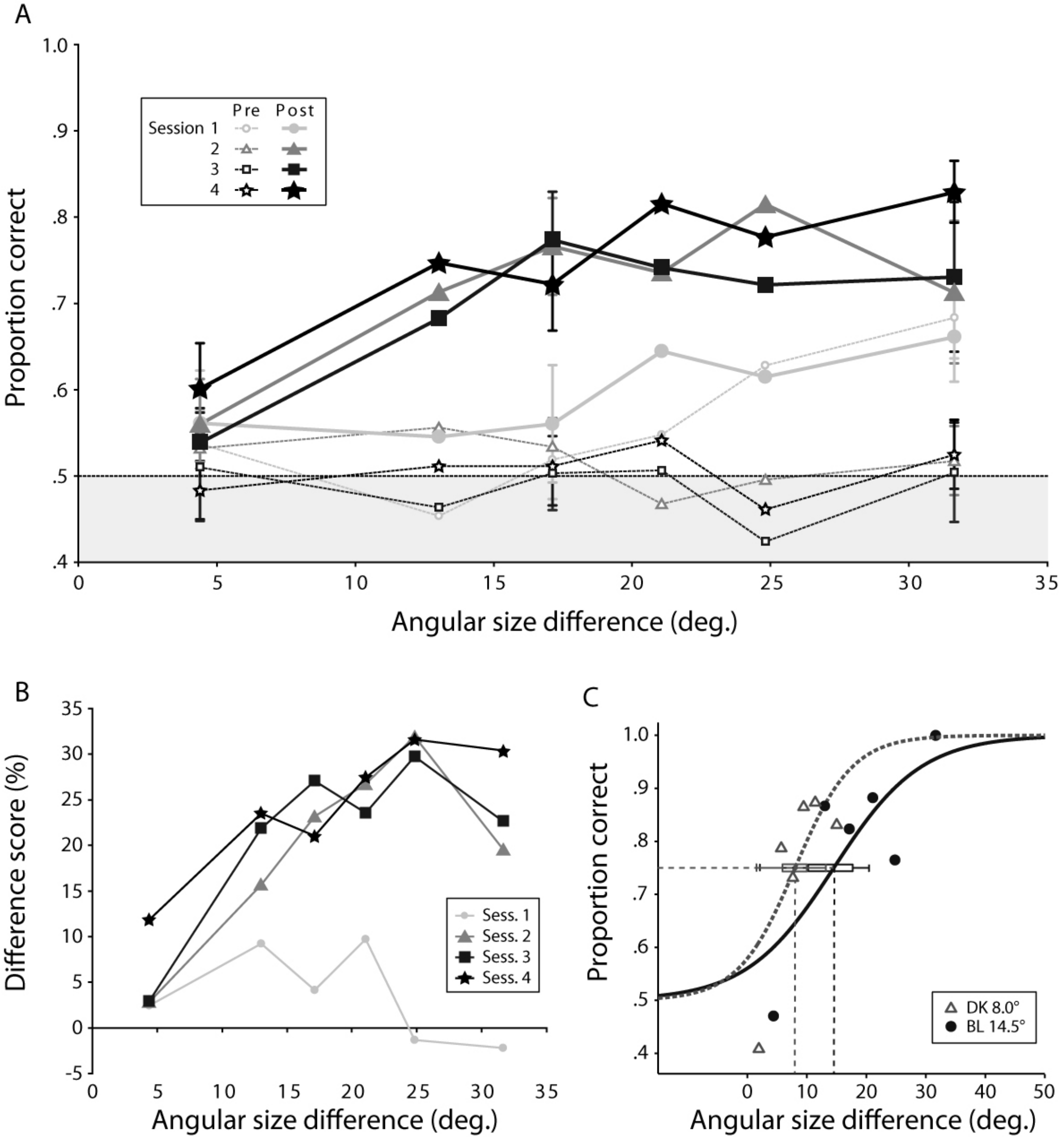


Figure 4-3. Experiment 1 results. (A) Size-discrimination performance for 8 sighted subjects over 4 sessions at a distance of 33 cm. Solid lines and filled symbols indicate postclick (echolocation) discrimination judgments; open symbols and dashed lines indicate preclick (baseline) judgments. Group preclick performance across sessions did not significantly differ from chance for any condition (all p_{Bonf}>.05). Error bars represent SEM. (B) Difference scores (postclick minus preclick) showing the performance benefit of echolocation increasing across sessions. (C) Representative single-session size-discrimination data and 75% discrimination thresholds from sighted subject BL (distance 33 cm) and expert echolocator DK (distance 75 cm). The threshold was 14.5° for BL, very close to the sighted group asymptotic threshold of 16.9° (panel A), and 8.0° for DK. Horizontal error bars represent bootstrapped 95% confidence intervals.

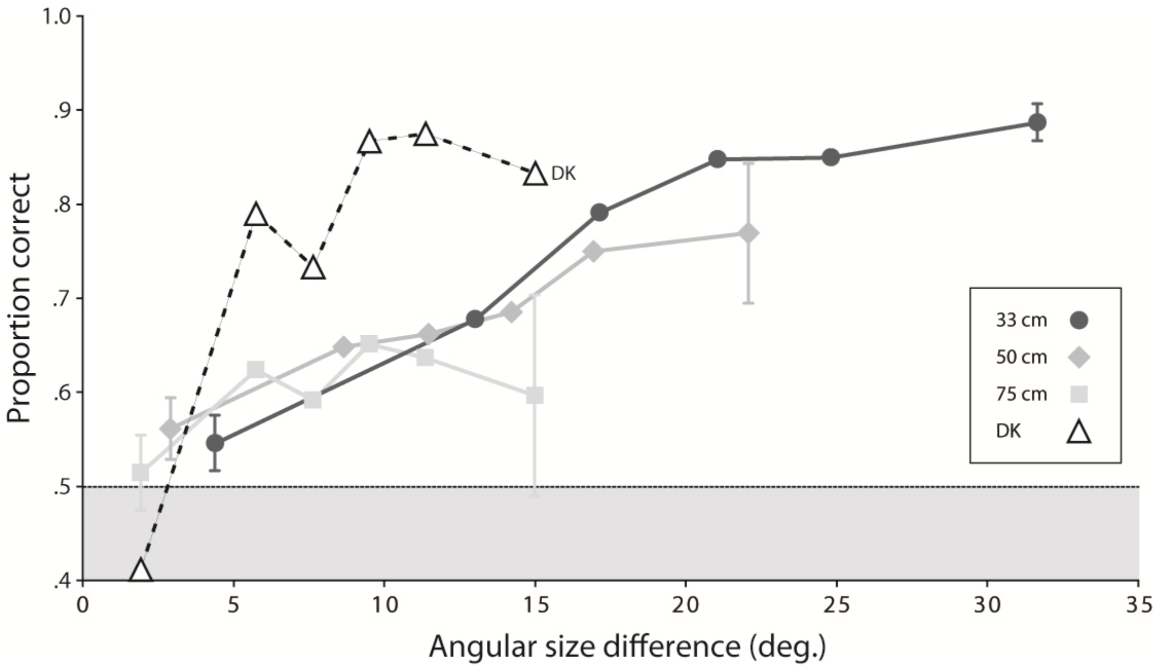
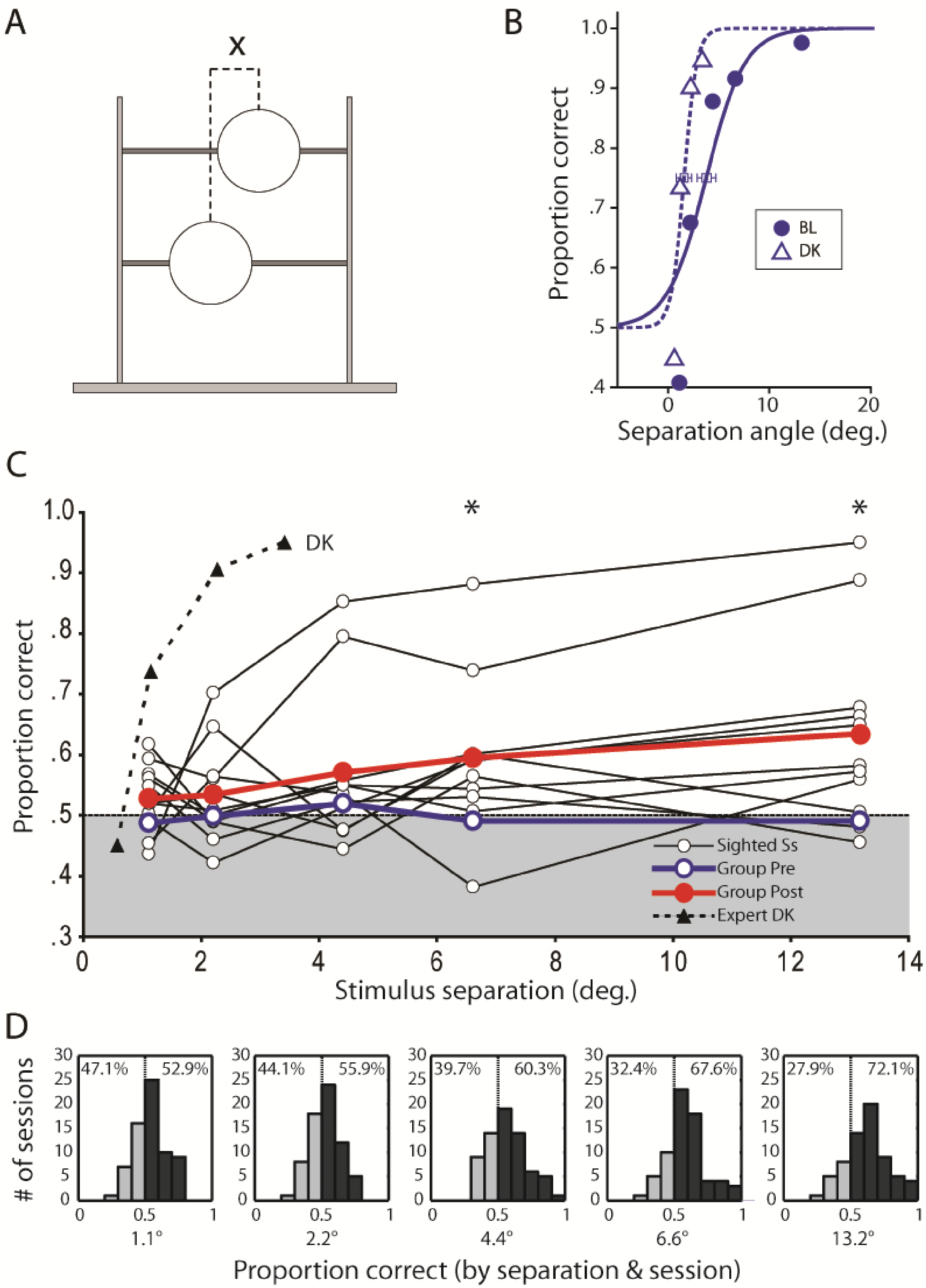


Figure 4-4. Distance effects on size discrimination. Solid curves represent asymptotic performance (averaged over 3 sessions) for 4 subjects at distances of 33 (circles), 50 (diamonds) and 75 cm (squares). Expert DK's single-session data at 75cm is shown for comparison. Representative error bars indicate 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 indicates performance regime below 50% correct.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Group Post
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12
14
Stimulus separation (deg.)
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25
20
15
10
5
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52.9%
44.1%
55.9%
39.7%
60.3%
32.4%
67.6%
27.9%
72.1%
0
0.5
1
1.1°
2.2°
4.4°
6.6°
13.2°
Proportion correct (by separation & session)

Figure 4-5

(Previous page)

Figure 4-5. (A) Stimulus setup for Experiment 2. Equal-sized stimuli were displaced horizontally from a central axis; the total horizontal displacement *x* between centers subtended a range of auditory angles from 1.1° to 13.2°. (B) Vernier acuity data for sighted subject BL and expert echolocator DK. The psychometric function for BL represents the average of four sessions at a distance of 50cm. DK's echolocating vernier acuity was measured at a distance of 100 cm. The 75% threshold was 1.58° separation between stimuli for DK and 3.76° for BL (after additional sessions, BL's average rose to 4.1°; see main text). (C) Group performance on Experiment 2 vernier displacement echolocation task. Solid blue circles indicate sighted subjects' group preclick performance, at chance for all separations. Solid red circles indicate group postclick performance. Individual postclick performance of all subjects is indicated by open circles. For comparison, open triangles indicate single-session data from expert echolocator DK (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 performance 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.

a. Spatial resolution estimated from active self-generated echoes

Study	N_blind	N_sighted
Kellogg, 1962, Science	2	2
Welch, 1964, Am. Foundation for the Blind	0	0
Rice et al., 1965, J. Experimental Psychology	5	0
Rice & Feinstein, 1965, Science	4	0
Rice, 1967, Science	5+4+6+4	0
Rice, 1969, Psychological Record	6+8	8+3
Ashmead et al., 1989, Perception and Psychophysics	10+15	0

b. Navigation, passive, and nonspatial discrimination tasks

Study	N_blind	N_sighted
Supa et al., 1944, Am. J. Psychology	2	2
Worchel & Dallenbach, 1947, Am. J. Psychology	10	0
Cotzin & Dallenbach, 1950, Am. J. Psychology	2	2
Worchel et al., 1950, J. Exp. Psychology	34	0
Worchel & Mauney, 1951, J. Exp. Psychology	7	0
Worchel & Berry, 1952, J. Exp. Psychology	0	15
Ammons et al., 1953, Am. J. Psychology	0	20
McCarty & Worchel, 1954, New Outlook for the Blind	1	0

Kohler, 1964, American Foundation for the Blind	0	267+20+48
Bassett & Eastmond, 1964, J. Acoustical Society of America	0	1
Juurmaa, 1969, Scand. J. Rehabilitation Medicine	52	0
Juurmaa, 1970, New Outlook for the Blind	0	0
Juurmaa & Suonio, 1975, Scand. J. Psychology	10	5
Hausfeld et al., 1982, Perceptual and Motor Skills	1	18+18+45
Strelow & Brabyn, 1982, Perception	8	14
Dufour et al., 2005, Exp. Brain Research	12	20
Despres et al., 2005, Brain Research	0	15+30

Table 4-1. 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.

5. Fine spatial acuity of echolocation in blind echolocation experts

Introduction

When vision is unavailable or insufficient for perception, other sensory modalities often take precedence in sampling the environment. In the case of echolocation — used, for example, by many bats and some marine mammals as a mechanism for navigation, object perception, hunting, and social communication (Thomas et al., 2004) — this sampling is active, taking the form of self-generated auditory pulses whose reflected echoes are then interpreted to generate surface and object percepts. To a limited extent, active echolocation has also been demonstrated in some humans, whose putative "facial vision" or "obstacle sense" was found to be auditory, not tactile in nature (Supa et al., 1944; Worchel and Dallenbach, 1947); whose performance was aided by active sounds versus passive hearing (Supa et al., 1944; Teng and Whitney, 2011); and who were able to detect, localize and discriminate some stimuli under various conditions (Gagnon et al., 2013; Hausfeld et al., 1982; Kellogg, 1962; Rice, 1967; Rice and Feinstein, 1965; Rice et al., 1965; Thaler et al., 2011). However, the behavioral envelope of human echolocation, and thus its potential mechanisms and range of utility, remains poorly understood. In particular, it is a reasonable working hypothesis that the spatial acuity of echolocation is critical to the object recognition and navigation tasks performed on a daily basis by highly trained, blind expert practitioners. Some echo tasks have shown localization using detection (Rice, 1969) or lateralization paradigms (Dufour et al., 2005; Thaler et al., 2011); despite this, no standardized measure exists by which to assess echoic spatial resolution. In vision, the Snellen chart (Snellen, 1863) is a common tool for acuity assessments; more powerful measures, probing finer scales of spatial discrimination, include Vernier acuity — a relative position judgment of two objects (Kniestedt and Stamper, 2003; Westheimer, 1979). In this study, therefore, we investigated the spatial resolution of echoic object localization in highly trained blind experts using an auditory analogue to the Vernier task.

Methods

Subjects

We recruited a sample of seven blind human echolocators with the aid of World Access for the Blind, a non-profit organization devoted to teaching echolocation techniques (Table 1). All participants gave verbal and written informed consent, and all were compensated for their time in accordance with guidelines set forth by the Committee for Protection of Human Subjects at the University of California, Berkeley. One participant was excluded from analysis by our criterion of defining highly trained echolocators as those who, by self-report, have at least 10,000 h of echolocation training experience, including both formal training and daily normal use. Six highly trained echolocators remained in the sample, with estimates of training time (combining formal training and daily use) ranging from approximately 12,000 h to over 200,000 h. Only one participant had any light perception abilities, and all reported using echolocation frequently as an aid in their daily lives.

Stimuli and procedure

Subjects' echo vocalizations were generated via trains of single-pulse tongue clicks with a typical clicking frequency of approximately 1-3 Hz. By emitting these self-generated tongue clicks from a fixed distance, subjects evaluated the relative positions of two identical, circular flat plastic discs, arranged vertically on a frame and separated horizontally by varying amounts (Fig. 5-1a). The discs, 20.3 cm in diameter and 6.35 mm thick, were coated with a thin layer of primer to ensure a uniform, matte reflecting surface. The frame consisted of a wooden base and two wooden dowels supporting two crossbars separated vertically by 27.5 cm. The hooks on the discs' rear surfaces allowed rapid removal and replacement in different configurations, and the crossbars were marked with 1 cm gradations. Participants were seated 50 cm from the discs, measured orthogonally from the ears to the plane formed by the discs, at a height such that their ears were halfway between the crossbars supporting the rods. Due to accessibility considerations, sessions were conducted in participants' homes or similar quiet testing spaces. A large sound-absorbent foam surface, approximately 193 cm tall by 203 cm wide, was mounted on a frame approximately 1 m behind the testing apparatus to provide a consistent acoustic background behind the stimuli across different testing sites. Participants wore close-fitting eye masks for consistency across subjects and to control for the residual light perception retained by one participant. In each trial (see detailed procedure below), the experimenter placed one disc on each crossbar at a specific position to the left or right of center. The top disc was always displaced an equal and opposite distance from center as the bottom disc. The distance of the discs from the center on each trial was pseudorandomized. The horizontal center-to-center separation between discs was the independent variable manipulated in the experiment and subtended 1.1° to 13.2° auditory angle; to avoid ceiling effects, the three participants with the best performance were seated farther away from the apparatus, their ears 100 cm from the disc plane, such that the discs subtended 0.57° to 3.4°(thus making the task more difficult). A shoulder tap signaled the beginning of the trial for the subject.

The task, a two-alternative-forced choice (2AFC) discrimination task using the method of constant stimuli, was to determine whether the top disc was positioned to the right or left of the bottom disc (Fig. 5-1b), using only clicking. We conducted two sessions with participants, each consisting of 80 trials and lasting approximately 1-2 h. During the first (practice) session, subjects gave two responses per trial: an immediate response without clicking, then a response after producing clicks. The immediate responses served as a control to establish that subjects were unable to use ambient sound to perform the task, i.e., that the clicks were necessary to make the judgments. The same dual-response method with one expert and a larger pool of sighted blindfolded participants had confirmed the utility of the clicks in a previous study, with subjects remaining at chance levels of performance without clicking. (Teng and Whitney, 2011). Thus, in the second session, participants made only a clicking judgment. During repositioning of the stimuli between trials, a padded foam and cardboard screen shielded the stimulus frame, and any associated auditory cues that might have been generated, from the participant. While clicking, participants were allowed to translate their head vertically, but monitored to ensure a constant distance from the stimulus rig. For one participant (S07), data were collected as part of our earlier study but reanalyzed here, with an 80-trial session in which four angular separations subtended 0.57° to 3.4°. For this participant, the two-response procedure was used in the second session as well as the first. One participant (S03) was confused about the task during the first 20 trials, so those trials were excluded from analysis; including these trials or removing this subject from the group analysis had no influence on the overall pattern of results. Feedback regarding accuracy and the actual displacement from center of the discs (in cm) was given for each trial.

Functionally, echolocation for blind practitioners is similar to vision in that it serves to generate a spatial representation of the environment. We therefore found it appropriate to make a direct comparison, using the same apparatus, of the discrimination performance achievable by auditory (echoic) and visual modalities. Using the same apparatus described above (Fig 5-3a), four sighted, psychophysically naïve volunteers with normal (n=2) or corrected-to-normal (n=2, eyeglasses) vision made visual judgments of the discs' relative positions in a single session of 120 trials. Though not compensated, each gave informed consent to participate according to UC Berkeley human subject research protection protocols. Subjects sat 50 cm from the plane of the discs, with the left eye covered by an eyepatch, and fixated monocularly straight ahead. The frame was situated 35° right of the midline (see Fig. 5-3a) against a matte black background under normal laboratory lighting conditions, such that the white discs were visible at high contrast (96.7%). In each trial, as in the echo experiment, subjects judged whether the top disc was to the left or right. Between trials, the rig was occluded by a handheld screen while the experimenter replaced the discs. The discs were situated at a large eccentricity because visual acuity varies greatly across the visual field: central vision is extremely fine, with minimum angles exceeding 5 seconds of arc for foveal vernier judgments e.g. (Levi et al., 1985) and 1 minute of arc for reliable recognition of visual objects such as letters (Kniestedt and Stamper, 2003). Due to this magnification factor, we presented visual targets at 35° eccentricity (Anstis, 1974), which is expected to yield visual acuity measures that approximate the acuity measured in the echoic vernier acuity experiment (see RESULTS).

Analysis

We fitted psychometric curves to results from individual sessions. The curve fitting procedure, implemented in the psignifit toolbox for Matlab 7.1 (The Mathworks, Natick, MA), utilized a maximum-likelihood method and the Weibull function for generating the underlying shape of the fitted curve (Wichmann and Hill, 2001a). Performance was measured as percent correct and constrained to range from 50% to 95%, with the 75% intercept chosen as the threshold. Confidence intervals were generated based on 10,000 simulations using psignifit's BC_a bootstrapping method (Wichmann and Hill, 2001b). A similar curve fitting procedure was used in the visual vernier comparison experiment. However, as we anticipated a lower lapse rate for this less strenuous task (see PROCEDURE above), performance for this comparison was allowed to range from 50% to 100%.

In calculating correlations between age of blindness onset, blindness duration, and echolocation acuity, we used a nonparametric test (Spearman's rho) to avoid violating normality, linearity, and homoscedasticity assumptions due to the small sample size. We then bootstrapped each subject's vernier threshold 10,000 times and fit a regression line to each iterated set of six thresholds. The values of the resulting 10,000 regression slopes yielded significance estimates for the correlation (Fig. 5-2): fewer than 0.5% were negative.

Additionally, group averages were obtained by computing the mean of each of 10,000 sets of individual subjects' bootstrapped thresholds and finding the median value of the resultant distribution.

Results

The six participants performed robustly above chance, with a mean bootstrapped 75% threshold of 3.46° auditory angle, as measured from the coronal plane of the ears (Figure 5-1A). The three best performers exhibited thresholds of less than 2°, superior to previous reports of blindfolded sighted (Teng and Whitney, 2011) subjects performing the same task and blind individuals performing other tasks of spatial localization (Kellogg, 1962; Rice, 1969; Rice et al., 1965; Thaler et al., 2011). Interestingly, there were substantial and systematic individual differences between our subjects, raising the question of whether early blindness might predict performance. Confirming this, we found a significant correlation between age of blindness onset and echolocation acuity ($n = 6$, Spearman $\rho = 0.94$, $p < 0.01$; see Fig. 5-2). A correlation between blindness duration and acuity did not reach significance; nor did a correlation between acuity and estimated echolocation training time. Of course, age and duration of blindness covary, so future studies are necessary to disentangle whether age or experience are the critical factors for the extraordinary precision of echolocation found here.

In our monocular visual vernier comparison experiment, four psychophysically naïve, sighted participants achieved a group mean 75% threshold of 1.4° at an eccentricity of 35°. This is comparable to the echo-acuity thresholds obtained by some of the blind subjects.

Discussion

The results here demonstrate remarkably precise spatial acuity of echolocation in expert practitioners. From a pragmatic standpoint, it is worth noting that even the later blind echolocators in our group achieved a relatively high degree of spatial precision and reported using echolocation functionally on a daily basis. Thus, individual differences in echolocation (or visual) acuity do not preclude the use of echolocation (or vision) in daily life. The spatial resolution of the best human echolocators we tested exceeds that of various previous human echolocation studies (Kellogg, 1962; Rice, 1969; Rice et al., 1965; Thaler et al., 2011) and compares favorably to several tests of artificial echolocation devices (Collignon et al., 2007; Hughes, 2001), though variation in methods makes direct comparison difficult. Additionally, it is comparable to that of other species known to rely heavily on echolocation for spatial object perception and navigation behaviors (Moss and Surlykke, 2010; Pack and Herman, 1995). In a previous investigation into echo acuity in the big brown bat, *Eptesicus fuscus*, the angular separation between brass rods was manipulated (Simmons et al., 1983). The 75% performance threshold of the bats in that experiment was approximately 1.5° horizontal angle when measured in a comparable fashion (2AFC localization) (Simmons et al., 1983), compared to the 1.2°-1.9° thresholds of the three best performers in our study. Thus, the subset of human echolocators who were blind from an early age show spatial resolution comparable to that observed in a species with specializations for echolocation.

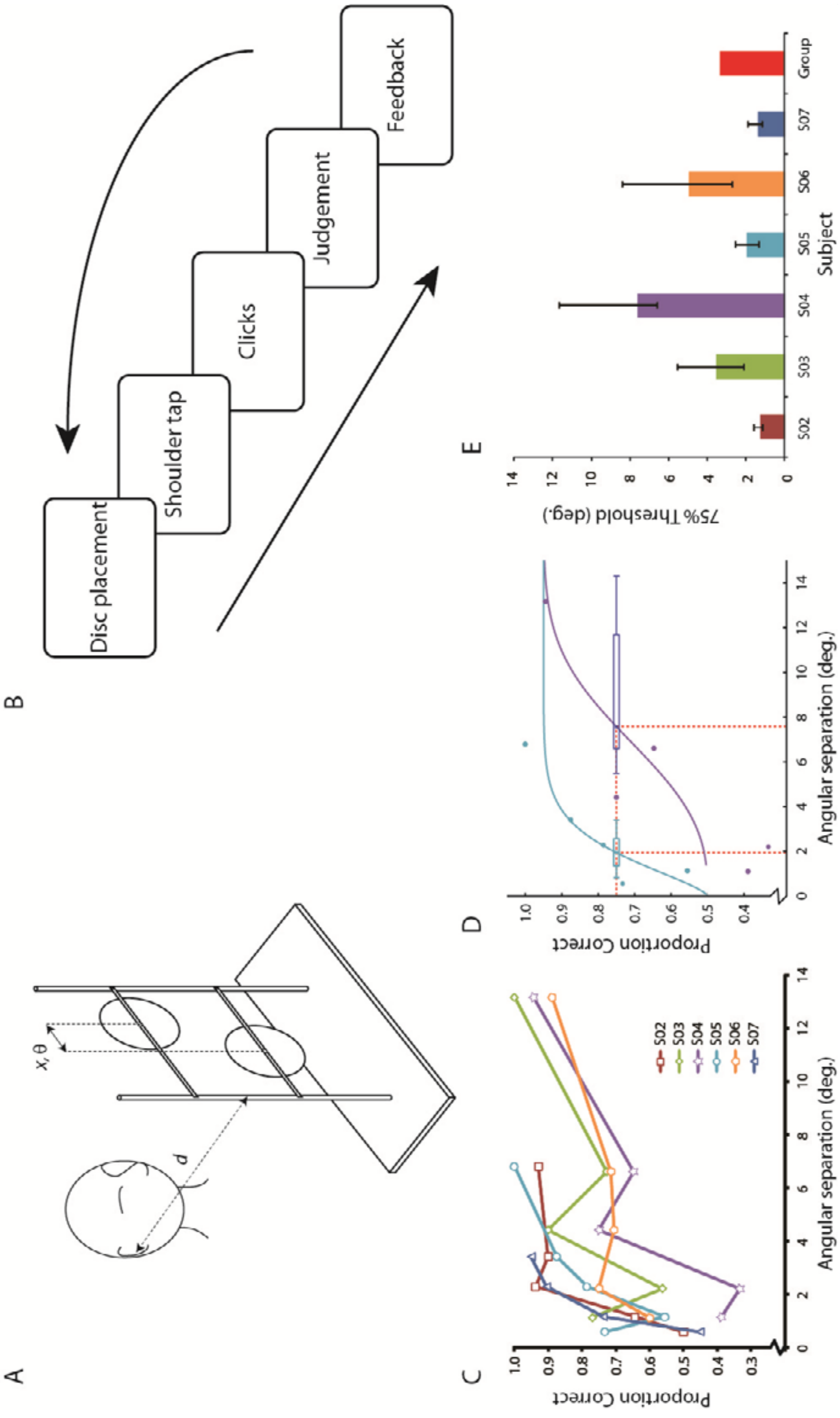
Although based on a small group of participants, the correlation in Fig. 5-2 suggests that early blindness plays a role in achieving the most precise levels of echolocation. This would be consistent with previous evidence of superior passive auditory performance in the blind compared to the sighted, early- versus late-blind individuals (Gougoux et al., 2005; Lessard et al., 1998; Muchnik et al., 1991; Röder et al., 1999), and recent echolocation results in 2 participants (Thaler et al., 2011), though the interplay of experience, practice and age of blindness remains open to further study.

These results indicate both superior echolocation acuity in blind expert practitioners compared to previous studies as well as a strong tendency toward higher precision with earlier blindness onset. This pattern of results may have several causes. For example, participants who had been blind from an early age, or for an extended duration, could plausibly have been proficient at the detection of echo cues but might lack the additional benefit of intensive, specific training in *active* echolocation. The novel vernier offset task could also have provided a more precise test of spatial echolocation acuity than tasks used in prior studies. Indeed, the vernier task analogue in the visual modality is a standard method of precisely and reliably measuring the acuity of vision; likewise, we believe that our vernier acuity measure of echolocation ability can provide a standard measure of the spatial resolution of echolocation acuity. Although our measurements were conducted in the medial plane, where passive spatial hearing acuity is known to be at its finest (Blauert and Allen, 1997; Middlebrooks and Green, 1991), this is also true of many previous human and non-human studies (Kellogg, 1962; Rice and Feinstein, 1965; Rice et al., 1965). Studies in which some form of echolocalization was conducted at large eccentricities off the medial plane indicate increased difficulty and decreased performance at those eccentricities (Rice, 1969; Thaler et al., 2011). Because the echolocation pulse is directional, it is likely that echoic vernier thresholds at greater eccentricities would be higher than those reported here.

The underlying cues mediating human echolocation performance remain unclear and are likely task-dependent; possibilities include binaural (interaural level and time difference) cues, monaural spectral features, and interference “ripples” (Arias and Ramos, 1997; Bassett and Eastmond, 1964; Carlson-Smith and Wiener, 1996; Rice, 1967; Simmons et al., 1983). Regardless of the particular cues involved, our implementation of a standardized approach for measuring spatial resolution has revealed that humans possess a remarkably precise spatial resolution of echolocation—more precise, for example, than would be predicted by simply calculating the wavelengths sampled by the peak-energy frequencies of typical echolocation clicks (Rice, 1967; Rojas et al., 2009a).

The resolution attained in our group of volunteers corresponds approximately to typical *visual* acuity at a retinal eccentricity of 35° (Anstis, 1974), measured here using the same stimuli and procedure, but with monocular visual judgments made by sighted observers (Fig. 5-3b).This comparison is instructive because it indicates that the spatial scale of the information afforded by vision to make the vernier judgment is comparable to the spatial scale of the information afforded by echolocation to make the same judgment. Our results therefore suggest that the usefulness of visual vernier misalignments at 35° eccentricity may extend to echolocation as well; they raise the intriguing possibility that traditionally visual functions — including object and scene recognition, visually guided behavior, and navigation — that occur in the peripheral visual field might also be available, with spatial resolution as high as vision, based on echolocation cues.

At present, few blind individuals are known to have formal training in the use of active echolocation. However, it is clear that this skill could be utilized much more extensively within the blind community, with practitioners achieving much higher resolution than previously recognized, potentially subserving fine object discrimination in addition to navigation. In light of that, the vernier acuity method presented here may provide a useful operational measure of the spatial resolution of echolocation.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Disc placement
Shoulder tap
Clicks
Judgement
Feedback
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S07
Group
Subject

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Figure 5-1. (A) Experimental setup for vernier echolocation discrimination. The stimulus frame was situated such that the normal distance between the plane of the discs and the ears was *d*. For 3 participants, *d* = 50 cm, and for 3, *d* = 100 cm. The auditory angle subtended, θ, was calculated by using the center-to-center horizontal separation between discs, *x*. At a distance of 50 cm, θ was between 1.1° and 13.2°; at 100 cm, it ranged from 0.57° to 3.4°. *x* was always between 1 and 12 cm. (B) Structure of one trial. While the experimenter placed the discs at the appropriate separations on the frame, a barrier prevented auditory cues from informing subjects about the location of the discs. The barrier was then removed, and a shoulder tap signaled the subject to begin clicking. The subject then made a judgment and received feedback. Sessions consisted of 80 trials and five stimulus separations. (C) Performance vs. angular separation between discs for six subjects. Chance performance was 50%. (D) Calculation of 75% performance thresholds. Two representative psychometric functions are shown, from subjects S04 and S05. Confidence intervals were generated with psignifit's BC_a bootstrapping method, running 10,000 simulations. (E) Thresholds plotted for each subject and group average. Individual subjects' error bars are bootstrapped standard deviations; group average is the median of the distribution of individual subjects' bootstrapped and averaged thresholds (see METHODS for details).

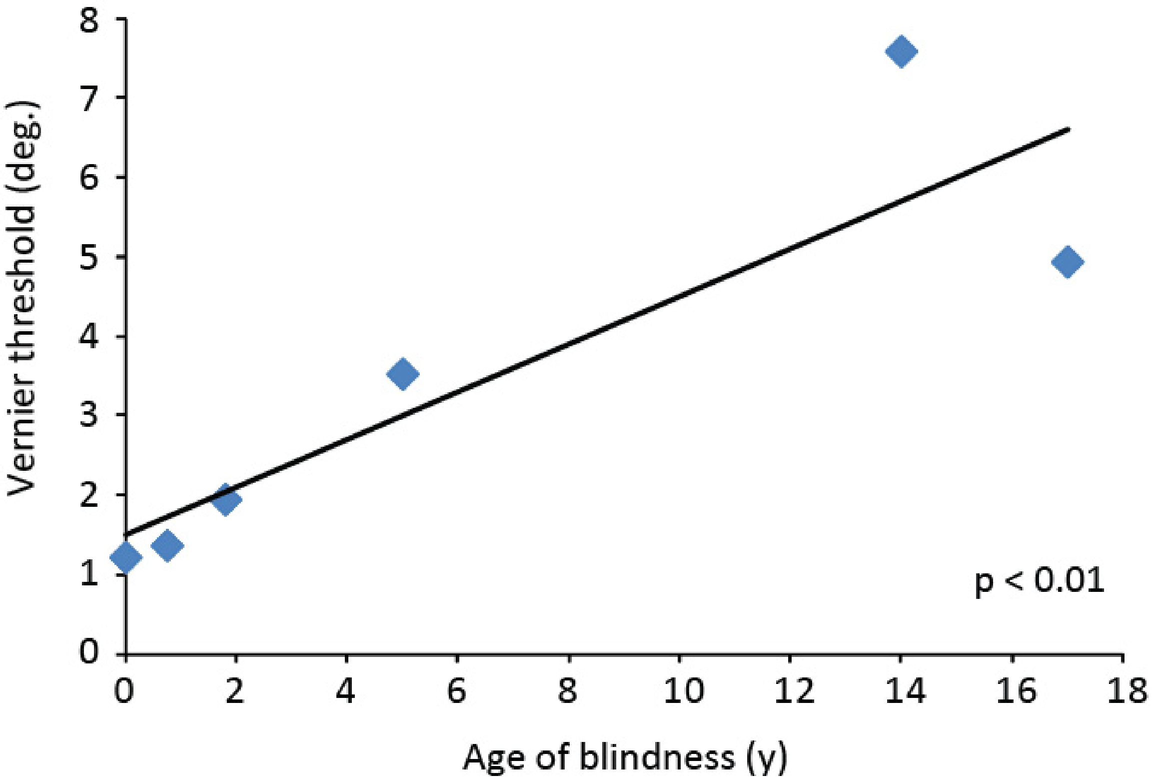

Figure 5-2. Correlation between vernier echo acuity and age of blindness onset, in years. N = 6, Spearman ρ = 0.94. Bootstrapped confidence intervals (see METHODS) yield $p < 0.01$.

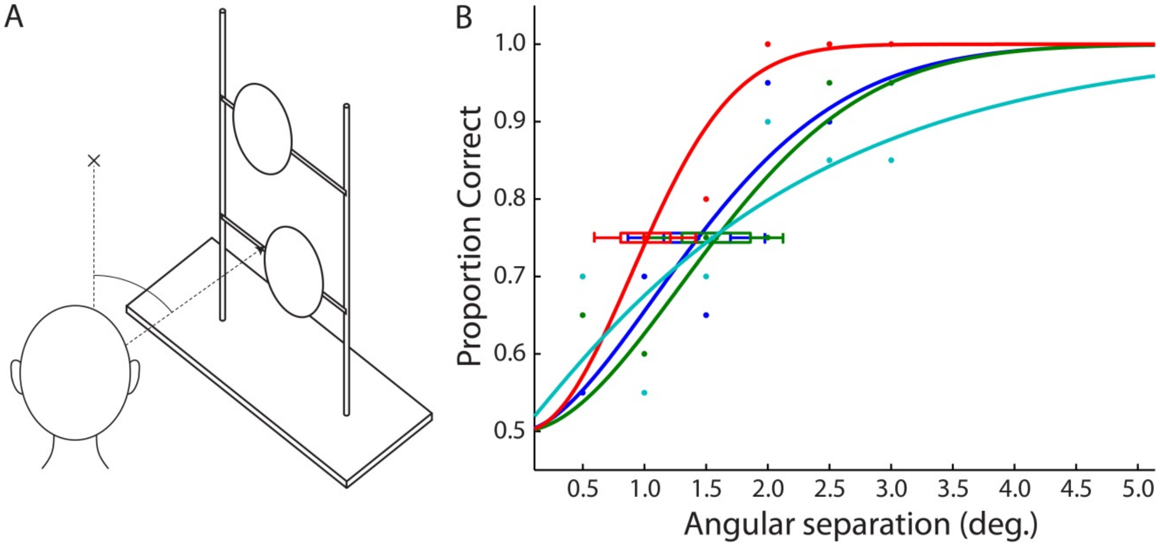

Figure 5-3. Visual vernier thresholds from 4 sighted naïve subjects at 57 cm distance and 35° retinal eccentricity. The same stimulus setup from the echolocation experiment (Fig. 5-1A) was used to present pairs of discs with vernier offsets ranging from 0.5° to 3.0°, in 0.5° increments. Sessions consisted of 120 trials — 20 at each of six separation conditions, randomly interleaved. Between trials, a screen occluded the stimulus frame. Subjects fixated a point and viewed the stimulus monocularly. One experimenter placed discs during each trial; another monitored subjects' gaze to ensure fixation. The group average 75% threshold was 1.4°.

Table 5-1	Sex	Age of blindness (yrs)	Cause of blindness	Age when tested (yrs)	Vernier threshold (deg)
S02	M	0	Glaucoma	28	1.22
S03	M	5	Retinitis pigmentosa, juvenile macular degeneration	25	3.52
S04	M	14	Optic nerve atrophy	27	7.58
S05	M	1.8	Retinoblastoma	33	1.94
S06	M	17	Familial exudative vitreoretinopathy	22	4.93
S07	M	0.75	Retinoblastoma	41	1.36

Table 5-1. Summary of subjects, causes of blindness, age and echolocation acuity.

6. Characteristics of human echolocation

The echo emission: Clicks

In the most commonly reported (Kish, 2003; McCarty and Worchel, 1954; Rice, 1967; Rojas et al., 2009b; Teng et al., 2012; Teng and Whitney, 2011; Thaler et al., 2011; Wallmeier et al., 2013) active echolocation technique, practitioners produce brief mouth "clicks" in which the tongue is pressed against the palate or alveolar ridge of the mouth, then drawn off that surface to produce a distinct single "oral vacuum pulse" (Rojas et al., 2009b). The sound produced is a discrete pulse with 60-100 dB intensity (Arnott et al., 2013; Schörnich et al., 2012), typically broadband in nature and lasting approximately 3-20 ms, though parameters vary considerably across and within participants and trials. Clicks are produced at typical estimated rates on the order of 0.5-4 Hz (Schörnich et al., 2012; Teng et al., 2012; Walters, 2013), and are used by practitioners to orient themselves, detect obstacles, and identify objects and surfaces.

Rojas and colleagues (Rojas et al., 2009b, 2010) conducted a series of analyses on some physical properties of various candidate echolocation sounds. The analyses were limited to visual spectral and waveform inspections and did not include psychophysical performance data. Several naturally and artificially produced sounds were recorded and analyzed. The authors concluded that palatal clicks, a dampened sinusoid waveform, were the ideal echolocation stimuli. However, they presented no performance data.

It is unclear, and remains a matter of some debate, how click duration affects performance on echolocation tasks. Schenkman and Nilsson (2010), Rowan et al. (2013), and Papadopoulos et al. (2011) varied the length of echolocation clicks generated artificially in echo-detection and localization tasks and found that longer emissions yielded better performance. The explanation proposed was Gibsonian (cf. Gibson, 1986): a longer pulse meant that more information was propagated through the "auditory array," providing more informative cues for task performance. However, naturally developed echolocation pulses are predominantly short clicks (Schörnich et al., 2012; Teng et al., 2012; Thaler et al., 2011; Wallmeier et al., 2013). It is likely that optimal echo information depends on the task being performed.

Eavesdropping and artificial echo pulses

Given the utility of echoes from both self-generated as well as artificial, externally generated sounds, might an echolocator make use of incidental echoes from another person's vocalizations? Such a practice, known as "eavesdropping," is well described in the bat and dolphin literature (Balcombe and Fenton, 1988; Dechmann et al., 2009; Gregg et al., 2007) but has not been explored in humans.

Indirect evidence suggests that, at least to a limited extent, echo cues produced by one person can be used by another. Echo clicks and returns recorded with binaural in-ear microphones have been used successfully for psychophysics even when recorded and played back in different people (Arnott et al., 2013; Schörnich et al., 2012; Teng et al., 2012; Thaler et al., 2011; Thaler et al., 2013; Wallmeier et al., 2013). Artificially generated echoes have also been used to perform echoic detection and discrimination tasks (Kohler, 1964; Rice, 1967).

Auditory cues supporting human echolocation

Since the fundamentally auditory basis of echolocation was firmly established, significant progress has been made in identifying the specific cues on which human echoic perception rests. Still, remarkably little consensus exists in many respects; a common refrain among past investigators has been an acknowledgment that systematic psychoacoustic studies have been lacking. Stoffregen and Pittenger (1995) proposed several possible cues available to an echolocator, including derivations from physical parameters of various situations; however, these were essentially hypothetical, with no direct tests of these hypotheses. Where does the information lie?

Papadopoulos and colleagues (Papadopoulos et al., 2011) conducted a series of analyses investigating the acoustic properties of an emitted pulse and its reflected echo. Using a head and torso simulator, they measured binaural cues contained in the reflected echo from an emitted pulse while varying the lateral position, distance, and orientation of a flat board relative to the simulated listener. The results suggested a strong dependence of binaural level cues (and thus information available for perceptual localization) on these factors. The predictions generated by the measured cues were largely borne out by psychophysical experiments (Rowan et al., 2013), in which subject performance decreased markedly as interaural time difference cues became less available.

Schenkman (2010) proposed the involvement of repetition pitch and loudness discrimination as cues informing the judgments of subjects in an echoic present-absent task. The change in these variables to values difficult to discriminate (e.g., repetition pitch below 40 Hz and loudness differences below 0.5 dB) correlated roughly to performance drops in blind and sighted subjects, but the authors did not manipulate these variables directly. Additionally, the superior performance of blind compared to sighted subjects was not explained in terms of these variables other than speculation that the blind subjects might have learned to discriminate them more finely.

7. Possible mechanisms and cues for human echolocation

Echolocation systems in bats are known to contain neurons specialized for echoic target distance, culminating in a cortical distance map (Portfors and Wenstrup, 1999; Riquimaroux et al., 1991). No evidence for such specialization in humans has been reported, but the advent of neuroimaging investigations of echolocation has begun to shed light on its physiological and acoustic underpinnings.

Visual cortex plasticity in blindness

A sizeable and growing body of literature implicates the occipital cortex in the performance of nonvisual tasks in the blind. The specific modes of reorganization remain poorly understood, but electrophysiological and neuroimaging studies have demonstrated a wide variety of tasks in which occipital regions are recruited. Such effects are typically not found in sighted participants performing the same tasks (but see Merabet et al., 2008). The remarkable variety of nonvisual tasks in which occipital cortex activity has been demonstrated in blind persons includes Braille reading (Cohen et al., 1997; Sadato et al., 1996), sound localization (Gougoux et al., 2005), verb generation (Amedi et al., 2004; Burton, 2003), verbal memory (Amedi et al., 2003), and object shape recognition through auditory sensory substitution (Amedi et al., 2007).

While a full review of crossmodal plasticity in occipital cortex is beyond the scope of this review (see Collignon et al., 2008; Kupers and Ptito, 2013; Merabet and Pascual-Leone, 2010; Pascual-Leone et al., 2005) there is widespread and converging evidence that the occipital cortex, deprived of its primary sensory input stream, undergoes plastic change, both functional and structural (Lepore et al., 2010; Pascual-Leone et al., 2005; Shimony et al., 2006), such that it responds to input from nonvisual modalities (Buchel et al., 1998; Sadato et al., 1996). The computations performed there are poorly understood, but it is known that they are functionally important: disruption, whether through stroke (Hamilton et al., 2000) or application of TMS pulses (Amedi et al., 2004; Cohen et al., 1997; Hamilton and Pascual-Leone, 1998), reduces performance on Braille reading tasks.

The foregoing may be critical to understanding echolocation and the tendency for superior performance in blind populations. Does echolocation in blind humans recruit visual areas as well? The circumstantial evidence described above suggests so. Active echolocation is inherently a motor task involving muscles of the tongue, throat and neck. However, fMRI studies are very susceptible to even the slightest head motions, which degrade the scan signals.

Neuroimaging of echolocation

The most direct investigations to date of the neural correlates of echolocation in humans have been a series of fMRI studies in which expert echolocators listened to binaural recordings of their own own echo emissions (clicks) in the presence and absence of various reflecting objects, and in anechoic vs. reverberant environments (Arnott et al., 2013; Thaler et al., 2011; Thaler et al., 2013). Thaler et al. (2011) demonstrated BOLD activation in the calcarine sulcus of blind echolocation practitioners when they listened to their clicks recorded in the presence of reflecting objects, i.e., when they heard echoes in addition to their own emitted pulses. Simply hearing the pulses without a reflecting object present did not elicit this activity, nor did hearing the echoes played back for a sighted control subject.

These neuroimaging results provide some tantalizing glimpses into potential underpinnings of human echolocation, though data obtained from relatively few echolocating individuals raises new questions. For example, as is often the case with fMRI studies, causal links between BOLD activations and associated echolocation performance remain to be elucidated. Thaler et al. (2011) report on two subjects, an early-blind (EB) and a late-blind expert echolocator LB. Unlike EB, subject LB demonstrated non-topographic calcarine BOLD activation in response to echo stimuli. That is, LB's calcarine sulcus did produce a BOLD signal in response to echoic stimuli, but it did not proceed rostrally with increasing echo eccentricity, nor did it show a preference for contralateral echoes. LB's chance-level performance during an echoic object localization task (Arnott et al., 2013) would be consistent with the idea that echoic objects are represented topographically in the primary "visual" cortex of a blind echolocator. However, LB was able to perform quite well at a separate echoic localization task, albeit with larger thresholds than EB (Thaler et al., 2011). This could suggest that the brain regions driving spatial echolocation performance are somewhere other than the calcarine sulcus, that EB and LB have differentially organized spatial representations, or that the calcarine activation has functions other than topographic representations. Clearly, as Thaler and Arnott themselves point out, further research is needed to clarify these and other ambiguities.

The functional nature of crossmodal plasticity: what is being processed?

There is a possibility that the recruitment of occipital cortex for echolocation in blind persons reflects enhanced spectral processing. A series of positron emission tomography (PET) studies of auditory spatial processing in blind persons showed that the best blind performers of a monaural vertical localization task recruited extrastriate occipital regions to a degree correlated with task performance (Gougoux et al., 2005). Consistent with the notion that vertical localization in humans is mediated largely by spectral (rather than binaural difference) cues (Recanzone and Sutter, 2008), these superior performers also performed better on a spectral discrimination task in which the spatial location of the stimulus was held constant (Voss et al., 2011). Interestingly, increased blood flow in occipital cortical areas was associated with better performance in blind subjects, but not in the sighted. While Voss et al. (2011) did not investigate echolocation, their results suggest the possibility that spectral auditory information, processed in the occipital cortex, may contribute to echo judgments made by blind persons.

Schenkman and Nilsson (2011) manipulated pitch and loudness information in an echoic detection task. Performance suffered somewhat when loudness information was removed, but considerably more so when pitch information was removed. In that condition alone, blind subjects' performance dropped to the level of sighted subjects performing the same task. The authors concluded that pitch information was critical to echo detection and suggested that higher sensitivity to pitch differences in the blind could explain the tendency toward higher auditory acuity compared to the sighted. However, it is important to note that their task was strictly one of detection, rather than localization, recognition, or other task that may well use different cues.

Echolocation and the precedence effect

Active echolocation is a special application of hearing, but human auditory systems routinely process echoes in other ways. In reverberant environments, incoming sounds often arrive at the listener's ear multiple times – a direct sound, followed closely by one or more echoes from nearby surfaces. The auditory system segregates the direct energy from a sound source from its echoes when assigning a location to an incoming sound. In what is known as the precedence effect (Fitzpatrick et al., 1999; Litovsky et al., 1999), the perceived location of the sound source is assigned to the leading sound, while the lagging sounds – the echoes, which contain spurious spatial cues – are suppressed. The delay between the lead and lag sound is on the order of 20 ms or less (Fitzpatrick et al., 1999; Litovsky et al., 1999; Papadopoulos et al., 2011), though influenced by variations in environment, stimulus characteristics, neuronal response properties and listener experience. This temporal scale corresponds to approximately 6.8 m of sound propagation, a comparable spatial scale to the operational range of human echolocation (Figs. 3-1, 3-2).

The critical difference between echo suppression and active echolocation is that in the latter case, the observer (emitting a direct echolocation pulse) is always the initial sound source. The echoes are the most informative portion of the signal, rather than a cue to be suppressed. Additionally, multiple echo returns could contain useful information rather than interfere with accurate localization. Thus, one would expect echo suppression to be counterproductive to the echoic localization and detection of objects. Empirical results in echolocating animals are scant but tend to bear out this prediction. Schuchmann et al. (2006) demonstrated that two species of echolocating bats failed to orient reliably to the first of two artificial echoes separated by up to 12.8 ms, consistent with a lack of echo suppression. In a conference proceeding, Zaslavski (2008) reported very fine localization thresholds in a bottlenose dolphin discriminating between two closely spaced artificial clicks or noise bursts. The dolphin reliably discriminated lead-lag separations as small as 0.25° and delays as small as 20 µs for correlated clicks as well as uncorrelated noise bursts, which was interpreted as an absence of echo suppression that would have perceptually fused the sounds.

Very recently, Wallmeier et al. (2013) reported an attenuation of the precedence effect in humans performing a virtualized active echolocation task, compared to a passive lead-lag listening task. Sighted subjects listening passively discriminated lead sounds much better than lag sounds, consistent with echo suppression. However, when actively echolocating two virtual objects, the leading and lagging echoes were equally difficult to discriminate, suggesting a "release from precedence." These results constitute the most direct investigation to date of echolocation and the precedence effect. They suggest rapid task-based shifts in echo processing and add to the body of evidence supporting echolocation facility in sighted persons. Still, it remains to be seen how precedence and echolocation interact in blind persons, who are generally more sensitive to echoes (Dufour et al., 2005; Kolarik et al., 2013), and particularly in practicing echolocators, who may have more specialized perceptual or cognitive systems in place for echo processing.

Future research on the processing and neural mechanisms underlying echolocation in humans should include studies that permit more directly causal hypotheses. One intriguing possibility is the use of TMS, which has previously been instrumental in establishing the functional relevance of crossmodal plasticity in blindness (Amedi et al., 2004; Cohen et al., 1997). Repetitive TMS (rTMS) to extrastriate occipital cortex in blind participants has been demonstrated to selectively impair spatial hearing as well as performance with a visual-to-auditory sensory substitution device, while sparing intensity and pitch discrimination (Collignon et al., 2007). Sighted subjects were not affected by the same stimulation. TMS to occipital cortex can also induce somatotopically organized tactile sensations in the fingers of Braille readers (Ptito et al., 2008) and the tongues of TDU (tongue display unit) sensory-substitution device users (Kupers et al., 2006). Again, only blind subjects reported these effects, strongly suggesting a functional reorganization of function specific to blindness, possibly dependent on an individual's specific experience. Somatosensory qualia resulting from "visual" cortex stimulation was interpreted by the authors (Kupers et al., 2011) as support for cortical deference to peripheral inputs (rather than cortical dominance). In other words, the subjective modality experienced by a person from activity in a given cortical region is dependent on the inputs to that region, rather than some inherent modality. This logic predicts that TMS applied to a blind echolocator's occipital cortex could induce "echo phosphenes" rather than visual phosphenes – an intriguing hypothesis for future study.

8. Summary

The literature and experiments presented here indicate that active echolocation can provide useful, readily available, and precise information for navigation and object perception. In particular, in contrast to equivocal earlier results regarding sighted subjects (cf. comparison between Ammons et al., 1953; Kellogg, 1962), proficiency on a spatial echolocation task such as size discrimination is available to sighted subjects within a few sessions of practice, though performance does not immediately match levels achieved by a blind expert (Teng and Whitney, 2011). However, this learning is task-dependent and subject to large individual differences: on a vernier relative localization task, wide variability and overall low performance was observed, while a sample of expert practitioners produced fine spatial thresholds approaching the theoretical limit of spatial hearing and rivaling the resolution of peripheral human vision (Teng et al., 2012; Teng and Whitney, 2011). These and other measures additionally provide a potential means for standardizing the nebulous concept of "echolocation ability," which would prove useful yardsticks in applied training interventions. Additional elucidation of the useful cues and neural mechanisms supporting human echolocation would further aid potential training programs for congenitally as well as adventitiously blind persons.

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