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Review

A summary of research investigating echolocation abilities of blind and sighted humans

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ABSTRACT

There is currently considerable interest in the consequences of loss in one sensory modality on the remaining senses. Much of this work has focused on the development of enhanced auditory abilities among blind individuals, who are often able to use sound to navigate through space. It has now been established that many blind individuals produce sound emissions and use the returning echoes to provide them with information about objects in their surroundings, in a similar manner to bats navigating in the dark. In this review, we summarize current knowledge regarding human echolocation. Some blind individuals develop remarkable echolocation abilities, and are able to assess the position, size, distance, shape, and material of objects using reflected sound waves. After training, normally sighted people are also able to use echolocation to perceive objects, and can develop abilities comparable to, but typically somewhat poorer than, those of blind people. The underlying cues and mechanisms, operable range, spatial acuity and neurological underpinnings of echolocation are described. Echolocation can result in functional real life benefits. It is possible that these benefits can be optimized via suitable training, especially among those with recently acquired blindness, but this requires further study. Areas for further research are identified.

1. Introduction and background

Adaptation to sensory loss has been the focus of considerable interest in psychology and neuroscience. Visual loss is often, although not uniformly, associated with enhanced auditory abilities, and these may be partly a consequence of cortical reorganization and recruitment of visual areas for auditory processing (Collignon et al., 2009; Voss et al., 2004, 2010). Many studies have examined the role that echolocation can play in improving spatial awareness for those who have lost their sight. For blind individuals, audition provides the sole source of information about sound-producing objects in far space, and even silent objects can be located using reflections of self-generated sounds (Boehm, 1986; Rowan et al., 2013; Supa et al., 1944; Wallmeier et al., 2013; Welch, 1964). Some blind individuals develop echolocation skills to a high standard, and display remarkable spatial abilities. Thaler et al. (2011, described below) tested two blind participants who used echolocation in their daily lives when exploring cities and during hiking, mountain biking and playing basketball. McCarty and Worchel (1954) reported that a blind boy was able to avoid obstacles while riding a bicycle by making clicking sounds with his mouth and listening to the returning echoes. Echolocation may have functional benefits for blind individuals (Thaler, 2013), and the ability to echolocate can be improved by suitable training for people with normal hearing (Teng and Whitney, 2011).

Echolocation has also formed the basis of sensory substitution devices (SSDs). These devices use an acoustic (ultrasound) or optic source that emits a signal together with a receiver to detect reflections of the signal. The received signal is used to calculate the distance between the source and reflecting object using the time taken for the reflections to return to the source. The distance information is then converted into an auditory (or haptic) signal (Hughes, 2001; Kellogg, 1962). This assistive technology has been used to help increase the spatial awareness and independent

Abbreviations: BOLD, Blood oxygen-level dependent; D/R, Direct-to-reverberant ratio; ILD, Interaural level difference; JND, Just-noticeable difference; KEMAR, Knowles electronics manikin for acoustics research; MRI, Magnetic resonance imaging; PET, Positron emission tomography; SSD, Sensory substitution device

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mobility of blind people (for reviews, see Roentgen et al., 2008, 2009).

In this review, we summarize current knowledge regarding the acoustic cues used for echolocation, work concerning the range of distances over which echolocation is effective (referred to as the operable range), the types of features of objects that can be discriminated using echolocation, and the underlying mechanisms. We describe research that has investigated whether some acoustic cues are used more effectively by the blind than by the sighted, and argue that evidence for enhanced echolocation skills in blind listeners is reasonably strong, although there can be considerable overlap between the echolocation skills of blind and sighted people, following suitable training. Neural underpinnings of echolocation and areas for further research are discussed.

1.1. Early research investigating human echolocation abilities

The term echolocation was first used by Griffin (1944) to describe the outstanding ability of bats flying in the dark to navigate and to locate prey using sound. Echolocation has since been identified and extensively studied for other animals, including dolphins and toothed whales (Jones, 2005). In 1749, Diderot described a blind acquaintance who was able to locate silent objects and estimate their distance (see Jourdain, 1916), although at that time it was not known that sound was involved. Diderot believed that the proximity of objects caused pressure changes on the skin, and this led to the concept of 'facial vision'; the objects were said to be felt on the face. Further cases were identified of blind individuals who had this ability, and numerous theories were put forward about the mechanisms underlying the phenomenon. The blind individuals themselves were unable to account for their abilities, and none of the many theories provided a satisfactory explanation. Hayes (1941) described fourteen competing theories that attempted to explain facial vision in perceptual, sensory, or occult terms.

Soon after, a series of pioneering studies carried out in the Cornell Psychological Laboratory established that facial vision was actually an auditory ability (Supa et al., 1944; Worchel and Dallenbach, 1947; Cotzin and Dallenbach, 1950). In the first of these studies, Supa et al. (1944) asked blind and sighted blindfolded participants to approach an obstacle, report as soon as they were able to detect it, and stop as close as possible to the obstacle. When the ears were occluded, the ability to detect the obstacle and to judge its distance disappeared. Worchel and Dallenbach (1947) and Cotzin and Dallenbach (1950) further demonstrated that acoustic stimulation was necessary to perceive the obstacle, and a later study showed that anesthetizing the facial skin had no effect on the perception of obstacles (Köhler, 1964). Further studies confirmed that both blind and sighted participants were able to echolocate (Ammons et al., 1953; Rice, 1967; Worchel and Mauney, 1951; Worchel et al., 1950), and the notion of facial vision was replaced by that of echolocation.

Sound echoes may provide the listener with substantial information regarding the properties of distal objects, including the distance to the object, the shape, and the object's size (Passini et al., 1986; Stoffregen and Pittenger, 1995). This is discussed in more detail later in this review.

2. Acoustic cues, underlying mechanisms, and the operable range of echolocation

2.1. Characteristics of echolocation signals used by humans

Bats echolocate using biosonar: the emitted signals are mainly in the ultrasonic range, beyond the upper frequency limit of human hearing (approximately 20,000 Hz). This can provide the bat with a rich source of information about very small objects, such as insects, including size, position, and direction of movement. Many blind individuals also use self-generated sounds to echolocate, such as clicks produced by rapidly moving the tongue in the palatal area behind the teeth (Rojas et al., 2009), or sounds produced by mechanical means such as tapping a cane against the floor (Burton, 2000). The sounds produced by humans are, naturally, at least partly within the audible frequency range for humans, but usually contain strong frequency components in the upper part of this range (Schörnich et al., 2012; Rowan et al., 2013). Also, there is evidence that high-frequency components are useful for at least some aspects of echolocation (Cotzin and Dallenbach, 1950; Rowan et al., 2013).

Echolocation involves three successive types of sound at the listener's ears (Rowan et al., 2013): (i) the emission (self-generated sound) only, (ii) the emission and echo superimposed, or, for short emissions and distant objects, a brief silent gap, and (iii) the echo only. This is illustrated in the left panel of Fig. 1, which shows responses to clicks measured in the ear of an acoustic manikin by Rowan et al. (2013). Click spectra are shown in the right panel. Clicks produced by the echolocator are often of short duration, approximately 10 ms, and have a broad spectrum (Schörnich et al., 2012; Thaler et al., 2011). Sound levels range from 60 to 108 dB SPL, with maximum energy in the frequency range 6–8 kHz (Schörnich et al., 2012). For analyses of the physical properties of self-generated sounds used for human echolocation, see Rojas et al. (2009, 2010). They suggested that short sounds generated at the palate are the most effective for echolocation. However, this requires experimental testing. Findings from other studies have suggested that longer duration sounds are most effective. Rowan et al. (2013) found that the ability of normally sighted participants to identify the lateral position of a board using echoes improved as duration increased from 10 to 400 ms for an object distance of 0.9 m. Schenkman and Nilsson (2010) reported that echolocation detection performance increased as signal duration increased from 5 to 500 ms for normally sighted participants, and that blind participants could detect objects at farther distances than sighted participants when using longer duration signals.

2.2. Cues used for echolocation, and operable range

In this section we describe the currently known acoustic cues used for echolocation. Putative acoustic cues for echolocation as an active mode of perception include:

(1) Energy: the returning echo increases the overall energy at the listener's ears, if the sound intensity is integrated over a few tens of ms. This cue is sometimes referred to in the literature in terms of the subjective quality of loudness. The level of the echo relative to that of the emission may also provide a cue.
(2) The time delay between the emitted sound and the echo. This may be perceived "as such" if the delay is relatively long (a few tens of ms) or it may be perceived as a "time separation pitch" or "repetition pitch" (Bilsen, 1966) when the delay is in the range 1–30 ms; the perceived pitch is inversely related to the delay.
(3) Changes in spectrum of the sound resulting from the addition of the echo to the emission. Constructive and destructive interference lead to a ripple in the spectrum, the spacing between spectral peaks being inversely related to the time delay of the echo relative to the emission. This cue may be heard as a change in timbre or pitch and it is the frequency-domain equivalent of cue (2). In many cases it is not clear

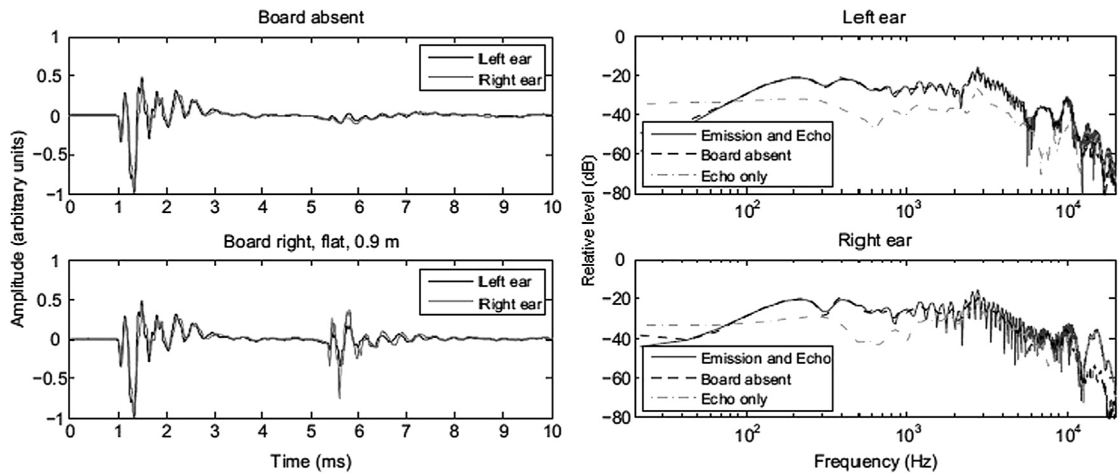

Fig. 1. Recordings of responses to clicks obtained using a KEMAR manikin, taken from the study of Rowan et al. (2013), their Fig. 2. The left panel shows waveforms, and the right panel shows their spectra, recorded in the presence or absence of a reflective board 0.9 m away, oriented so that its flat surface faced the manikin. The waveform of the emission is shown in the top-left panel; this is small after 4 ms. The bottom left-panel shows the emission, gap, and response associated with the echo from the board, which occurs just after 5 ms. Used with permission from Rowan et al. (2013).

whether analysis in the temporal domain or the spectral domain is critical.

(4) Differences in the sound reaching the two ears, especially at high frequencies. These can provide information about the orientation of objects. For example, when a flat board faces the listener, the signals are similar at the two ears, as illustrated in Fig. 1. If the board is at an oblique angle relative to the listener, the sound differs at the two ears, particularly at high frequencies.

(5) Differences in the reverberation pattern within a reverberant room. An obstacle within a reverberant environment will alter the pattern of reverberation, and lead to reflections with shorter delays.

The above list of cues is not necessarily exhaustive, as some cues that have been proposed for echolocation have not yet been demonstrated to be useful for humans. One such cue is echoic tau, which is a derived quantity that may be used to predict time to contact when the echolocator is approaching an object. It refers to the ratio (distance between the echolocator and the object)/(speed of approach). It is monotonically related to time to contact. The speed of approach may be estimated from kinesthetic and motor information about the speed of walking, while the distance may be estimated from one or more of cues 1–5. Echoic tau may provide an additional source of information to support echolocation; for example, if an echolocator moves so as to keep echoic tau constant, they will halt just as the object is reached (Stoffregen and Pittenger, 1995). Rosenblum et al. (2000) conducted a study with blindfolded sighted participants, who were required to use echolocation to detect a wall while either approaching the wall or standing still. The wall was then removed, and participants were asked to walk to the prior location of the wall. Accuracy in judging the distance of the wall was slightly higher for moving than for stationary echolocation for some wall distances, possibly due to use of time-to-arrival information based upon echoic tau. The use of echoic time-to-arrival information for controlling approach when moving was discussed by Stoffregen and Pittenger (1995), following evidence that echoic tau is used by echolocating bats (Lee et al., 1992). However, it has not been clearly demonstrated that echoic tau is used by humans.

Although this review focuses on active echolocation, we note that the term echolocation is sometimes used to describe navigation behaviors that rely on passive cues, which are not discussed in detail here. These include changes in the ambient sound field due to the buildup of sound pressure approximately a meter in front of a wall, which result in a shift in spectral balance towards lower frequencies. This shift may provide a cue that enables blind individuals to maintain a constant distance from a wall for safe travel (Ashmead and Wall, 1999).

Cotzin and Dallenbach (1950) investigated the role of pitch and loudness in echolocation. Steel wires were used to suspend a carriage with a loudspeaker and microphone that was moved toward an obstacle from various starting points using a soundproofed motor. The speed of approach was controlled by the participant. The stimuli were thermal noise (similar to white noise) or pure tones with frequencies ranging from 0.125 to 10 kHz. The sounds were picked up by the microphone and delivered to the participant's ears using headphones. The task was to stop the approach and report when the obstacle was first perceived, and then to move the carriage as close as possible to the obstacle without collision. All participants (sighted and blind) reported a rise in pitch of the thermal noise as the obstacle was approached that enabled them to perform the task. Performance was poor for pure tones with frequencies up to 8 kHz, but performance improved for the 10-kHz tone. For the thermal noise stimulus only, Cotzin and Dallenbach also tested whether perceived loudness increased when the carriage was nearer to an obstacle, and reported this not to be the case. They concluded that changes in pitch but not loudness for sounds containing high frequencies were necessary and sufficient for blind individuals to perceive obstacles. However, changes in pitch cannot account for the above-chance performance obtained with the 10-kHz tone. Presumably, performance in that case depended on constructive and destructive interference between the direct sound and the reflection, which led to marked fluctuations in level, especially an increase in level when the loudspeaker was very close to the obstacle. One participant reported "The tone becomes more piercing and shrill when it nears the obstacle" and another reported "The tone suddenly gets louder… it screams when near the obstacle."

Arias and Ramos (1997) investigated the role of repetition pitch detection and discrimination in an echolocation paradigm. They used stimuli composed of a "direct" signal (a click or burst of noise recorded at the output of a loudspeaker), presented either alone or together with a reflected signal or echo. The latter was either a real echo produced by a reflecting disc or was a delayed copy of the direct sound attenuated by 3.5 dB. Baseline delays of 2 ms and 5 ms between the direct and reflected signal were used. For such delays, strong repetition pitches are heard (Bilsen, 1966; Yost and Hill, 1978). The tasks included detecting the object (discriminating sounds with and without echoes), and discriminating changes in the distance between the sound source and the object, produced by varying the delay between the direct sound and echo from the baseline value. For the discrimination task, because repetition pitch varies inversely with distance, the presence of an obstacle closer to or farther from a reference position (corresponding to the baseline delay) would result in a higher or lower pitch being perceived, respectively, allowing participants to use repetition pitch as a cue. Participants were well able to perform both tasks. Note that in the condition with the original sound plus a delayed copy of the sound attenuated by 3.5 dB, the overall level and the relative level of the echo did not change when the distance (delay) was changed, but performance was good, suggesting that the absolute or relative level of the echo is not a critical cue for distance discrimination. Arias and Ramos (1997) suggested that repetition pitch was a good cue for detecting objects and discriminating their distance via echolocation.

Schenkman and Nilsson (2011) investigated whether level information (described by them as "loudness") or some other form of information (described by them as "pitch") was used in echolocation. Blind and sighted participants were asked to indicate which of two recordings of a noise burst (recorded using an acoustic manikin) was made in the presence of a reflecting disc. The recordings were presented in three conditions: (1) in their original form (all cues available); (2) with the level of the two recorded signals equated, so that the level cue was removed, but all other cues remained; (3) when both of the two signals presented in a trial were recorded in the absence of a reflecting disc, but one of the sounds was increased in level so as to simulate the level cue only. Their results when the distance to the disc was 2 m are shown in Fig. 2. The performance of both blind and sighted participants was worse when only the level cue was available than when the level cue was removed but other cues remained. The results suggest that the level cue plays a small role, but that other spectral and/or temporal cues are more important. The performance of blind participants was close to chance for objects at 3 m. The individual differences are discussed later.

The accuracy of echolocation by humans can depend upon object distance (Kellogg, 1962; Rice et al., 1965; Rowan et al., 2013).

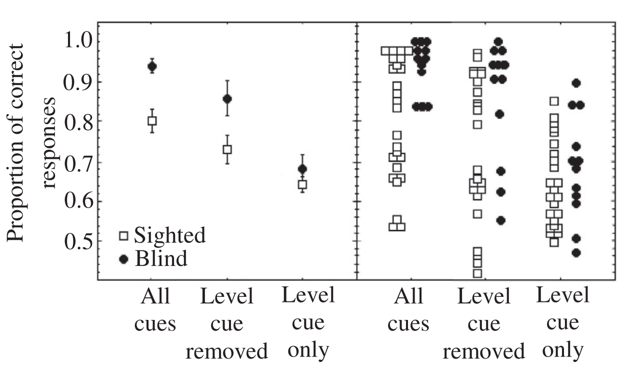

Fig. 2. Scores from the study of Schenkman and Nilsson (2011), showing the proportion of correct responses in judging whether a disc was present, based on echolocation. The distance to the disc was 2 m. The left and right panels show the mean and individual results, respectively. The conditions were: all cues, level cue removed, and level cue only. Redrawn from Figure 6 of Schenkman and Nilsson (2011).

Kellogg (1962) tested two blind individuals in an echolocation size discrimination task. One was able to perform well for object distances of 12 inches, and performance fell as the distance of the object was increased to 24 inches. However, no effect of distance was observed for the second blind individual tested. Rice et al. (1965) found that thresholds for detecting metal discs using echoes remained constant with distance. Rowan et al. (2013) found that accuracy in judging the lateral position of a board based on echolocation decreased with increasing distance, and for distances of 2 m and above the performance of both blind and blindfolded sighted participants was at chance. The lateral position of the board was more likely to be correctly identified in the 'angled' condition of Rowan et al. (2013), where the flat face of the board was positioned so as to reflect sounds directly toward the participant, in which case specular (mirror-like) reflection paths to both ears were present. Performance was lower in the 'flat' condition, in which the board's flat face was positioned so that specular reflections did not reach both ears of the participant. In this case, binaural cues were weaker and more complex for the majority of distances tested (Papadopoulos et al., 2011). Based on these results, Rowan et al. suggested that judgments of lateral position were dependent upon high-frequency binaural cues such as interaural level difference, or ILD (Papadopoulos et al., 2011), although the possibility that participants used monaural changes in level at the ears was not ruled out.

Changes in the pattern of reverberation in a room caused by a reflecting object may also act as a cue to echolocation, as the presence of an object will result in reflections with shorter delays. Schenkman and Nilsson (2010) found that the largest distance at which echolocation could be used was greater in a reverberant conference room than in an anechoic room. However the use of cues related to the pattern of reverberation may only be possible in rooms with relatively short reverberation times (see Section 5 for further discussion of this point).

2.3. *The information provided by echolocation regarding the position, size, material and shape of an object*

Echolocation can be used to judge and discriminate both the lateral position and distance of objects. Teng et al. (2012) measured echolocation acuity for discriminating the relative lateral position of two reflecting discs, using an auditory analog of the visual Vernier task, which involves judging the relative position of two objects (Kniestedt and Stamper, 2003). Teng et al. found that blind expert echolocators showed acuities of approximately 1.2° of azimuth, approaching the resolution of spatial hearing in the frontomedial plane. This low threshold reflects best performance among experts for this task, and may not be typical of acuity among the general population. For young, sighted, normally hearing participants, Schörnich et al. (2012) showed that echolocation just-noticeable-differences (JNDs) for distance were in general below 1 m. For a reference distance of 1.7 m, JNDs were generally less than 0.5 m.

Echolocation can also be used to judge the relative sizes of objects. Rice and Feinstein (1965) found that blind participants were able to use echoes to discriminate object size, and that their best-performing participants were able to discriminate objects with area ratios as low as 1.07:1. Since large objects reflect more acoustic energy than small objects, two cues that might be used for discrimination of size are overall sound level and sound level of the echo relative to that of the emission. However, level differences between the echoes produced by reflections from objects can occur not only as a result of differences in size, but also as a result of differences in the material from which the object is composed, distance between the echolocator and the object, and the shape of the facing surface (e.g. a flat vs. a concave surface). Stoffregen and

Pittenger (1995) suggested that size information may be obtained by combining information about delay, spectrum and level. The delay between the emission and echo can be used to determine the "expected" level difference between the emission and echo due to distance. Differences in spectrum between the emission and echo are determined by the type of material from which the object is composed (see below for details) and can be allowed for if the type of material is fixed over trials or is known in advance. Given this information, any remaining differences in level or spectrum between the emission and echo can be used to estimate the size of the object.

Objects made of different materials can be identified and discriminated using echoic information (DeLong et al., 2007; Hausfeld et al., 1982). Following training, blindfolded sighted participants were able to use echoes to distinguish objects made from fabric, plexiglass, wood, or carpet (Hausfeld et al., 1982). Participants reported using pitch and timbre changes to perform the task (DeLong et al., 2007; Hausfeld et al., 1982).

Materials differ in their absorption characteristics. For example, soft materials such as carpet tend to strongly absorb high frequencies, whereas rigid materials such as plexiglass reflect higher as well as lower frequencies. Hence, if the spectrum of the echo contains relatively less high-frequency energy than that of the emission, it can be inferred that the material is soft, whereas if the spectra of the echo and emission are similar, it can be inferred that the material is hard. Stoffregen and Pittenger (1995) proposed that object material may be identified using the relative frequency spectra of the emission and the echo, and it has been suggested that sound echoes contain sufficient acoustical cues in the frequency range below 3000 Hz to distinguish between several different wood surfaces (Rojas et al., 2012). However, it has not yet been demonstrated that these cues can be used.

While there is good evidence that echoes can be used to discriminate objects made of different materials, evidence for the identification of objects in isolation on the basis of echoes is weak. In studies that have investigated echo-based perception of materials, participants usually had to distinguish echoic information from successively presented materials or to identify the materials from a small possible pool of choices (e.g. Hausfeld et al., 1982). Further research is needed to investigate how many different types of materials can be distinguished, to assess the magnitude of the difference between materials needed to support accurate discrimination, and to determine whether echoic information can be used to identify objects in isolation.

Objects of different shapes that are matched in area and distance can also be distinguished using echoic information. Following training, blindfolded sighted participants were able to use echoes to discriminate the shapes of various objects, including circle, triangle, square, or no target (DeLong et al., 2007; Hausfeld et al., 1982; Rice, 1967). The cues underlying this ability remain somewhat unclear. Rice (1967) investigated the ability to detect (not discriminate) flat aluminum objects of different shape but identical surface area (31 cm^2) at a distance of 122 cm from the participant. Performance was best for a square and circle, lower for an oblong shape (4:1), and lower still for a longer oblong (16:1). The orientation of the oblong did not affect performance. Rice hypothesized that the decrease in performance as the target became longer and thinner was caused by a reduction of echo intensity, due to the specular reflection of energy away from the ears with increasing angle at which the signal struck the target. Hence, echo intensity provides a possible cue for discrimination of target shape, although presumably this cue would not be effective for absolute identification of target shape.

Rice observed that bending an oblong target, thus focusing echoes back toward the ear, increased the number of detections of the longer of the two oblong targets. Similarly, the concavity of a bowl will amplify returning echoes relative to those for objects with flat surfaces (Arnott et al., 2013). Hence, echo intensity also provides a potential cue for discriminating surfaces of the same shape and area, but different concavity. For objects that vary in concavity, the emission-to-echo delay will differ for parts of objects nearer to and farther from the participant, so changes in concavity will lead to changes in overall delay and spectrum of the echo. The extent to which these cues support concavity discrimination remains somewhat unclear.

3. Do blind individuals develop enhanced echolocation abilities?

3.1. A summary of research comparing echolocation performance of blind and sighted participants

Echoic information provides useful information regarding the surrounding environment (Kolarik et al., 2013c; Mershon et al., 1989), and blind individuals rely heavily upon this information for perceiving the spatial layout of their surroundings. In this section, we address the issue of whether blind people have superior echolocation abilities to sighted people. Various factors may contribute to the development of superior echolocation abilities in blind people, such as reliance on and extensive experience in using echoic information (i.e. increased practice), and crossmodal 'takeover' of visual cortex following visual loss, leading to increased cortical resources for auditory processing (see Section 4 for more details).

Some studies have demonstrated that blind people have higher sensitivity to non-self-generated echoic information than sighted controls (Dufour et al., 2005; Kolarik et al., 2013a). Dufour et al. (2005) showed that blind participants were more accurate than sighted controls in localizing an object using echoic information from sound generated by a loudspeaker, and were more sensitive to task-irrelevant echoes from a nearby lateral wall when localizing sounds in azimuth. Kolarik et al. (2013a) reported that blind participants were better able than sighted participants to perform a distance-discrimination task when only direct-to-reverberant ratio cues were available. However, not all studies reveal superior abilities of blind listeners in using non-self-generated sounds. Burton (2000) studied the use of cane tapping to determine whether a gap in a walkway could be crossed with a normal step while walking. In a condition designated 'sound only', the experimenter tapped the cane on the vertical faces on either side of the gap. Burton found no difference between blind and sighted participants for this condition. Several studies have reported that blind participants have echolocation abilities superior to those of sighted participants when using self-generated sounds (Clarke et al., 1975; Juurmaa and Suonio, 1975; Kellogg, 1962; Neuhoff, 2004; Rice, 1969; Schenkman and Nilsson, 2010, 2011). However, echolocation abilities within both the blind and sighted populations show considerable individual variability (Teng and Whitney, 2011; Teng et al., 2012; Rowan et al., 2013). Some sighted individuals, following training, achieved echolocation abilities similar to those of a blind expert (Teng and Whitney, 2011). Furthermore, echolocation abilities are very likely to be task dependent, and further research is needed to compare performance across blind and sighted groups for different echolocation tasks.

Schenkman and Nilsson (2010) measured accuracy in judging which of two recordings of a noise burst was made in the presence of a reflecting disc. On average, blind participants performed better than sighted participants, a finding replicated in a second study (Schenkman and Nilsson, 2011; as described in Section 2.2) and supporting previous work by Kellogg (1962). The superior performance of the blind participants was most apparent when the reflective disc was positioned between 2 and 5 m from the participant; all participants performed well for distances less than 2 m. As shown in Fig. 2, on average, the blind participants in Schenkman and Nilsson's (2011) study performed better than the sighted participants in all conditions. Scores varied widely across participants within each group, especially when not all cues were present. However, when all cues were available, the blind participants all achieved relatively high scores (84% correct or better), while some sighted participants scored close to chance (50% correct). Also, three blind participants made no errors when all cues were present, while none of the sighted participants achieved this. The scores for blind and sighted participants overlapped much more in the condition where only the level cue was available.

Since most studies comparing the echolocation abilities of blind and sighted participants have not reported audiometric thresholds, it is possible that some of the differences across groups were related to differences in audiometric thresholds. However, since the groups were usually reasonably well matched in terms of age, there is no obvious reason why audiometric thresholds should have differed across blind and sighted participants. Carlson-Smith and Weiner (1996) found no statistically significant correlation between high-frequency hearing sensitivity (measured by pure-tone thresholds at 8, 10, and 12 kHz) and echolocation performance (the detection of obstacles and doorways), although echolocation performance was related to the ability to detect changes in frequency and amplitude of low-frequency sounds. However, it may have been the case that all participants had sufficiently good hearing at high frequencies to make use of echoic information at those frequencies.

More generally, it has been suggested that enhanced auditory abilities in blind individuals may be due to an increased ability to discern pertinent acoustic cues (Voss et al., 2004). The greater reliance of blind people on acoustic cues in everyday life may improve the ability to use subtle cues, such as small differences in spectral envelope, and this may lead to more effective processing of acoustic spatial information (Voss et al., 2004), including information for echolocation. Spectral envelope variations lead to changes in perceived timbre that can be utilized to recognize objects or extract information regarding the environment (Ashmead and Wall, 1999; Au and Martin, 1989; Schenkman, 1986). Doucet et al. (2005) showed that blind participants were better able to localize sounds monaurally, presumably based on spectral cues resulting from reflections of sound from the pinna, suggesting superior abilities of the blind in processing spectral information. Enhanced spectral processing may extend to enhanced echolocation abilities among the blind.

In summary, the weight of evidence supports the idea that, on average, blind people are better echolocators than sighted people. It has been argued that while normally sighted individuals do echolocate, this is not necessarily a conscious process, and it occurs to a much lesser degree than for blind echolocators (Stoffregen and Pittenger, 1995; Schwitzgebel and Gordon, 2000). It remains somewhat unclear whether the best blind echolocators have superior skills to those of the best trained sighted echolocators. The extent to which takeover of the visual cortex for auditory processing contributes to the echolocation skills of blind people also remains uncertain; see below for further discussion of this point.

3.2. The effect of training on echolocation abilities

Although many blind people develop echolocation skills that they use to aid in navigation and object location, these skills vary substantially across individuals, and not all blind people can echolocate. Sighted people do not generally display echolocation

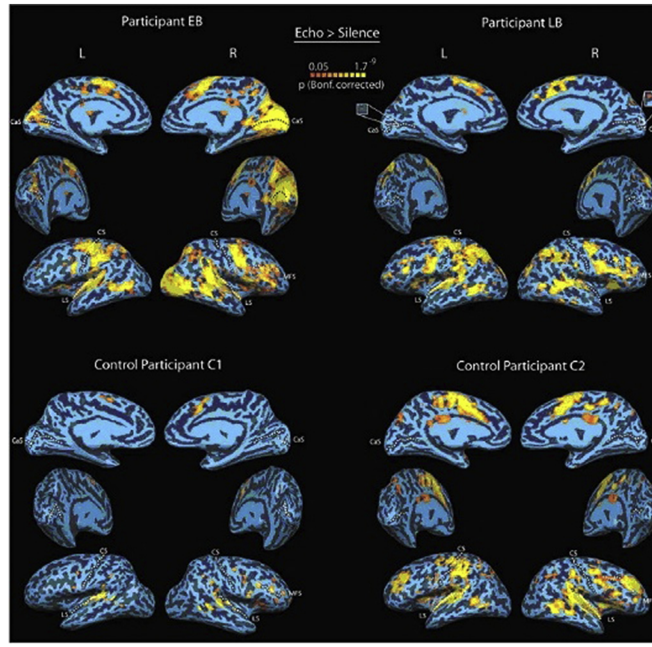

Fig. 3. Blood oxygen-level dependent (BOLD) activity projected on the cortical surface of participants from the study of Thaler et al. (2011), their Fig. 2. Concavities are colored dark and convexities are colored light. CS: central sulcus, CaS: calcarine sulcus, LS: lateral sulcus, MFS: middle frontal sulcus. The upper panel shows BOLD activity for blind participants EB and LB listening to recordings of their own echolocation sounds. The lower panel shows BOLD activity for sighted controls C1 and C2, listening to EB and LB's echolocation sounds, with which they had received prior training. There was clear BOLD activity in the calcarine sulcus, an area associated with visual processing, for the blind but not for the sighted participants. Used with permission from Thaler et al. (2011).

abilities without training, probably because visual signals provide substantially more accurate spatial information. Congenitally blind children are often able to use ambient auditory information to detect an obstacle, suggesting that no formal training is necessary to use sound to perceive objects if blindness occurs early in life (Ashmead et al., 1989). For blind participants, Teng et al. (2012) observed a strong correlation between age of onset of blindness and echolocation ability, consistent with improvements in performance produced by practice and/or by brain plasticity.

An important issue for future research is to establish whether systematic training can lead to the acquisition of echolocation skills among blind adults who have failed to develop such skills, and also to establish whether training can enhance the acquisition of echolocation abilities among those who have newly lost their vision (Schenkman and Nilsson, 2010).

4. Neuronal bases of echolocation

Little is currently known regarding the neural basis of echolocation, and whether the mechanisms subserving echolocation differ between sighted and blind individuals. In addition to the evidence for enhanced echolocation by blind people (Kellogg, 1962; Rice, 1969; Schenkman and Nilsson, 2010, 2011), as described above, there is evidence that blind people display enhanced abilities for auditory tasks such as sound localization (Lessard et al., 1998; Voss et al., 2004) and distance discrimination (Kolarik et al., 2013a; Voss et al., 2004). It has been proposed that functional recruitment of visually deafferented regions of the occipital cortex, an area that processes visual information for normally sighted individuals, may underlie these abilities (see Voss and Zatorre, 2012 for a review). If the echo-processing abilities of blind people partly reflect the recruitment of visual (occipital) areas of the brain, those areas should be activated during an echolocation task.

De Volder et al. (1999) used positron emission tomography (PET) to compare brain activity for early-blind and sighted participants who were trained to use an ultrasonic SSD to detect and evaluate the distance of an object. Activity in the occipital cortex was found to be higher for the blind than for the sighted participants. Higher activation was found in Brodmann areas 17, 18 and 19 for the blind but not for the sighted participants when the SSD was used to localize the object. Thaler et al. (2011) showed that functional magnetic resonance imaging (MRI) activity increased in the visual cortex of one early-onset and one late-onset blind participant (both experienced echolocators) when listening to sounds containing clicks and returning echoes, compared to the situation where sounds with no returning echoes were present (see Fig. 3). This activation was not observed for normally sighted, non-echolocating controls, even though they had received training listening to these sounds. No differences in activity in the auditory cortex were observed.

In a follow-up study, Arnott et al. (2013) investigated activation in the occipital cortex in response to shape-specific echo processing. Echolocation audio was recorded in an anechoic chamber or hallway using tongue-clicks in the presence of a concave or flat object that was covered either in aluminum foil or a cotton towel. For an early blind participant with extensive echolocation experience, blood oxygen-level dependent (BOLD) activity in ventrolateral occipital areas and the bilateral occipital pole was greater when the participant attended to shape than when they attended to the material or location of the object. Furthermore, feature specific echo-derived object representations were organized topographically in the calcarine cortex. A congenitally blind participant who began using echolocation comparatively later in life and a late-onset blind participant did not show the same type of activation, suggesting that extensive echolocation training at an early or critical age establishes echo-processing mechanisms in these brain areas.

Thaler et al. (2014) conducted an MRI study where BOLD activity was recorded while blind echolocation experts and normally sighted echolocation novices listened to binaural recordings of sounds. For one class of 'echolocation' sounds, the recordings contained both self-generated mouth clicks and echoes of the clicks reflected from an object. For the other class of 'source' sounds, the object emitted the sound and no echo was involved. The object was positioned either to the left or right of the participant and was either moving or stationary. Thaler et al. reported that temporal–occipital visual cortical areas were recruited for echo-motion processing for blind but not for sighted participants. They suggested that "echo-motion response in blind experts may represent a reorganization rather than exaggeration of response observed in sighted novices" and that "There is the possibility that this reorganization involves the recruitment of 'visual' cortical areas."

Overall, these results support the idea that visual cortical areas are recruited for auditory processing, including echolocation, in blind people. The extent to which such recruitment contributes to the echolocation abilities of the blind remains unclear. Normally sighted individuals can also echolocate, despite the absence of visual cortex recruitment for this group. It is not yet known whether brain areas that process echoic information for other auditory tasks, such as perceiving the distance of a sound source, are also activated during echolocation tasks. Sound echoes provide listeners with a primary cue to sound source distance (direct-to-reverberant ratio or D/R, Zahorik et al., 2005; Kolarik et al., 2013a, 2013b). A recent study in near space showed that neural populations in the planum temporale and posterior superior temporal gyrus were sensitive to acoustic distance cues including D/R, independent of level (Kopčo et al., 2012). It is possible that these areas are also activated during echolocation tasks for both normally sighted and blind individuals. However, this requires further study.

5. Concluding remarks and suggestions for further research

The studies described in this review have provided numerous insights into echolocation in humans. However, many aspects of echolocation are not yet understood, and the reasons for individual differences in echolocation ability have not been determined. Further work is needed to clarify what cues are used in the various aspects of echolocation, to establish the functional benefits of echolocation, to investigate the accuracy of locomotive guidance using echolocation, and to establish how the acoustic characteristics of the environment, such as background noise and reverberant energy, affect echolocation abilities. The effects of age of onset of blindness on echolocation abilities have only recently begun to be investigated in depth and the effects of hearing loss on echolocation have not been studied. These areas are discussed in the following paragraphs.

The acoustic characteristics of the environment, particularly background noise and reverberant energy present during sound emission, may affect echolocation performance. Background noise may make it difficult to perceive an object based on echoic information and to distinguish it from other objects, in a similar way that background noise can make it difficult to separate sounds based on their location (Moore, 2012). In reverberant rooms, room reflections may interfere with reflections from the target object (Schörnich et al., 2012). Background reverberation distorts the monaural spectrum, as well as the interaural level differences and interaural phase differences of sounds reaching the listener's ears (Shinn-Cunningham et al., 2005). Spectral distortions may particularly affect blind listeners, as spectral cues appear to play an important role in their ability to echolocate (Doucet et al., 2005).

Surprisingly, as mentioned in Section 2.2, Schenkman and Nilsson (2010) reported that echolocation was possible for objects at greater distances in a reverberant conference room than in an anechoic room, suggesting that a reverberant environment can actually enhance performance. The presence of a reflecting object will change the pattern of reverberation, and introduce shorter delays to the reflections, thus providing a potential cue. However, the reverberation time in the study of Schenkman and Nilsson (2010) was rather low ($T_{60} = 0.4$ s), and it is possible that longer reverberation times would lead to impaired rather than improved performance. Although the usefulness of some acoustic spatial cues, such as direct-to-reverberant ratio for distance discrimination, has been shown to depend upon reverberation time (Kolarik et al., 2013b), the effects of reverberation time on echolocation performance have yet to be quantified.

Echolocation abilities are often useful in navigating through outdoor environments (McCarty and Worchel, 1954), where the environmental conditions and absorption characteristics of the various obstacles encountered vary considerably. For example, snow absorbs sound, with the degree of absorption varying depending upon whether the snow is wet or dry (Albert, 2001). Thus, one might expect that echolocation would be generally less effective under snowy conditions. The effectiveness of echolocation in rainy or snowy conditions requires further investigation, in order to examine the conditions in which echolocation provides real benefits for navigation.

There has been little investigation of the accuracy with which echolocation information can be used to form internal representations for navigating safely through the individual's surrounding environment. As described above, echoic information can allow obstacles to be located at least crudely. However, precise motor responses must be made in order to avoid collisions, by walking around obstacles or across gaps, or safely moving through apertures. Hughes (2001) showed that echoic information from an SSD could provide sighted blindfolded participants with spatial layout information regarding the width of various apertures. In a study of Kolarik et al. (in press), blindfolded sighted participants were required to use echoic information from SSDs to rotate their shoulders and pass through apertures of various widths. Their results showed that the participants could indeed adjust their shoulder rotations depending on the width of the aperture. However, human echolocation signals provide less precise spatial information than SSDs, and human echolocation requires a comparison between self-generated sound and the echoes (Thaler et al., 2011). Further work is needed to investigate how useful human echolocation signals are for tailoring locomotor adjustments, such as shoulder rotations when passing through apertures and walking around obstacles during navigation.

Relatively few studies have investigated the effects of early versus late-onset visual loss on echolocation abilities (Thaler et al., 2011). However, the results suggest that early visual loss results in better echolocation. As noted above, Teng et al. (2012) found that age of onset of visual loss was strongly correlated with echolocation acuity in a group of expert echolocators. The study of Thaler et al. (2011), described above, showed that click-echo processing recruited visual brain areas in both early- and late-blind echolocation experts. The authors suggested that further work is needed to determine whether such recruitment occurs for normally sighted individuals who are trained to echolocate, and for blind individuals with 'regular' sensitivity to echoes who do not echolocate (blind novices). Whether individuals with partial non-correctable visual losses develop enhanced echolocation abilities remains to be tested. Evidence for sensory compensation in this group is mixed, with some studies showing improvement (Hoover et al., 2012), and others showing no improvement (Kolarik et al., 2013a; Lessard et al., 1998). There is some evidence that individuals who have partial correctable visual losses develop enhanced echolocation skills and a higher sensitivity to echo cues than normal-sighted controls (Després et al., 2005).

The consequences of hearing loss for echolocation abilities are currently unknown. This issue is especially important for older blind echolocators, who are at risk of hearing impairment. Rowan et al. (2013) reported that judgments of the lateral position of an object using echolocation were primarily based on information from frequency components above 2 kHz. Other studies suggest that useful cues for echolocation lie above 5 kHz (Cotzin and Dallenbach, 1950). Since hearing loss is typically greater at high than at low frequencies (Moore, 2007), echolocation abilities may be degraded as a consequence of hearing impairment. Carlson-Smith and Weiner (1996) reported that echolocation performance was not correlated with audiometric thresholds at high frequencies, which at first sight seems inconsistent with this idea. However, their subjects all had "normal" hearing. Although hearing aids partially compensate for loss of audibility at high frequencies, they do not necessarily restore the ability to discriminate high-frequency sounds. For example, they do not compensate for the effects of reduced frequency selectivity. Also, most hearing aids do not produce useful gain for frequencies above about 5 kHz. The effects of hearing impairment and hearing aid processing on echolocation remain to be explored.

Recent studies have investigated how auditory space emerges for blind individuals, and how this space is maintained in the absence of visual calibration cues (Lewald, 2002, 2013). Accurate spatial representations of auditory space are maintained among blind individuals, at least in the horizontal dimension (Lessard et al., 1998; Voss et al., 2004). This has been attributed to calibration based upon audiomotor feedback, which refers to the relationship between self-motion and systematic changes in auditory stimuli (Lewald, 2002, 2013), e.g. angle of head rotation and changes in interaural time difference and ILD cues for azimuthal localization. To our knowledge, echolocation has not yet been considered within this context. However, it seems plausible that echoic information may aid in the calibration of auditory space and especially of distance. This remains to be confirmed.

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