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Review

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

Andrew J. Kolarik [a,*], Silvia Cirstea [b], Shahina Pardhan [b], Brian C.J. Moore [a]

[a] Department of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, United Kingdom
[b] Vision and Eye Research Unit (VERU), Postgraduate Medical Institute, Anglia Ruskin University, Eastings 204, East Road, Cambridge CB1 1PT, United Kingdom

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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

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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

[*] Corresponding author. Tel.: +44 (0) 1223 333584; fax: +44 (0) 1223 333564.
E-mail addresses: ak771@cam.ac.uk, kolarikaj@googlemail.com (A.J. Kolarik), silvia.cirstea@anglia.ac.uk (S. Cirstea), shahina.pardhan@anglia.ac.uk (S. Pardhan), bcjm@cam.ac.uk (B.C.J. Moore).

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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