



Echolocation in humans: an overview

Lore Thaler^{1*} and Melvyn A. Goodale²

Bats and dolphins are known for their ability to use echolocation. They emit bursts of sounds and listen to the echoes that bounce back to detect the objects in their environment. What is not as well-known is that some blind people have learned to do the same thing, making mouth clicks, for example, and using the returning echoes from those clicks to sense obstacles and objects of interest in their surroundings. The current review explores some of the research that has examined human echolocation and the changes that have been observed in the brains of echolocation experts. We also discuss potential applications and assistive technology based on echolocation. Blind echolocation experts can sense small differences in the location of objects, differentiate between objects of various sizes and shapes, and even between objects made of different materials, just by listening to the reflected echoes from mouth clicks. It is clear that echolocation may enable some blind people to do things that are otherwise thought to be impossible without vision, potentially providing them with a high degree of independence in their daily lives and demonstrating that echolocation can serve as an effective mobility strategy in the blind. Neuroimaging has shown that the processing of echoes activates brain regions in blind echolocators that would normally support vision in the sighted brain, and that the patterns of these activations are modulated by the information carried by the echoes. This work is shedding new light on just how plastic the human brain is. © 2016 Wiley Periodicals, Inc.

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INTRODUCTION

Most of us have encountered a blind person navigating a busy street with the aid of a white cane or a seeing-eye dog. Some of us may have also encountered a blind person walking confidently along while making clicking noises with their tongue—avoiding obstacles and other people well before they are within reach of the long cane. It turns out that such an individual is using echolocation—the same skill that bats and dolphins use to navigate their environments. Using echolocation, bats, dolphins, and indeed some blind humans interpret their

respective worlds by listening to the echoes bouncing off objects and surfaces from the clicking noises they make.

Human echolocation is opening up a vibrant area of research in psychology and neuroscience. It is not only a fascinating subject in its own right, but it is providing a window into neuroplasticity, affording researchers a fresh paradigm for probing how the brain deals with novel sensory information.

Although there have been a number of previous reviews of human echolocation,^{1–3} the current review introduces the topic of human echolocation to a general audience. We hope it will generate interest and excitement in this burgeoning research area. Like previous reviews, we explore some of the research that has examined human echolocation, and the changes that have been observed in the brains of people who use echolocation on a daily basis. We also discuss potential applications and assistive technology based on echolocation.

*Correspondence to: lore.thaler@durham.ac.uk

¹Department of Psychology, Durham University, Durham, UK

²The Brain and Mind Institute, Department of Psychology, University of Western Ontario, Ontario, Canada

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HISTORICAL OVERVIEW

At one time, the ability that blind people showed in avoiding obstacles and not walking into walls, even without the use of a cane, was referred to as ‘facial vision’ or ‘obstacle sense.’ Scientists were not sure how it worked, but many believed that blind people were able to detect subtle changes in air pressure on their skin, particularly on the face, as they approached a wall or some other large obstacle. Initially, the ability to detect obstacles without vision was considered a special skill of a few blind people who were particularly sensitive to these cues. But a series of experiments conducted at Cornell University in the 1940s and 1950s made it clear that blind people were actually listening to the echoes of their own footfalls and other self-produced sounds bouncing off walls and other surfaces in their immediate surroundings.^{4–6} It was indeed changes in air pressure—but from sound waves from the echoes striking their eardrums! Subsequent research went on to show that both blind and sighted people can learn to avoid obstacles without vision, as long as they have normal hearing.^{7,8} In short, these studies showed that the ‘obstacle sense’ was not a mysterious skill of only a few blind people, but was instead a general ability that almost anyone could acquire. Interestingly, scientists continued to investigate the role of audition in navigation by the blind as late as the 1960s⁹ possibly addressing doubts the scientific community had about people’s ability to hear and interpret acoustic echoes.

The term echolocation was coined in 1944 by Donald Griffin, a physiologist at Harvard who was studying how some bats are able to avoid obstacles in the dark.¹⁰ Although such bats make sounds in the ultrasonic range, it soon became clear that some humans, particularly blind humans, can make use of audible sounds for example from their own vocalizations, tongue clicks, whistles, or footsteps to do the same thing. Initially, echolocation research in humans focused mainly on the detection of obstacles. Subsequent studies, however, progressed from obstacle detection tasks to measuring people’s ability to perceive the distance, direction, size, shape, and even the material properties of objects simply by listening to the echoes returning from these objects.^{9,11–16} The authors of those studies described a wide range of sonar emissions in participants, including whistles, hisses, and speech, in addition to clicks. Many early studies made use of ‘categorical tasks,’ which measured people’s ability to identify something from a limited number of alternatives. In the 1960s, Winthrop Kellogg introduced the psychophysical method

to human echolocation research, making more fine-grained measures of people’s echolocation abilities possible.¹²

Scientists have made progress in investigating the acoustic features that may be relevant for human echolocation.^{17–27} To date, research that systematically manipulated echo-acoustic features and measured effects on echolocation performance^{23–26} has focused on echoes from white (or bandpass filtered) noise signals generated electronically rather than on sonar emissions that people make. Furthermore, most of these studies have focused on the echolocating person as a ‘perceiver.’ Yet echolocation is an active process. In daily life, expert echolocators move their bodies and heads around while they echolocate—and the nature of these movements appears to be influenced by their goals and intentions. In many ways human echolocators are perhaps behaving like bats which ‘steer their sound beam’ to sample different objects and surfaces as they fly through their environment.²⁸ In fact, recent investigations of blind humans who echolocate have shown that movement is an essential component for successful identification and localization of objects.^{29–31}

The tradeoff (and conflict) between laboratory control and ecological validity is an issue not unique to echolocation research. Nevertheless, because the use of echolocation offers an important opportunity for improving mobility in blind people, it is important to bridge the gap between laboratory research and real-life applications.

THE SONAR EMISSION

In early studies, the sounds (i.e., sonar emissions) that blind (and sighted) people made to generate the returning echoes were not systematically controlled, such that people were free to use any emission they wanted. The emissions used included talking, whistling, humming, mouth clicks, footsteps, a tapping cane, and other noises. Although many types of emissions may be used for echolocation, more recently (i.e., since 2011) there has been increased interest in echolocation using mouth clicks. The mouth clicks tend to be 3–15 ms long^{27,32} with peak frequencies ranging from 3 to 8 kHz. Figure 1 shows waveforms and spectrograms of some clicks and echoes made by human expert echolocators (see the figure caption for more details). Figure 1 visually illustrates that echoes carry information about the spatial environment. For example, Figure 1(a) and (c) shows that when a sound reflecting object is located off to the right, the echo is stronger in the right ear as compared to that

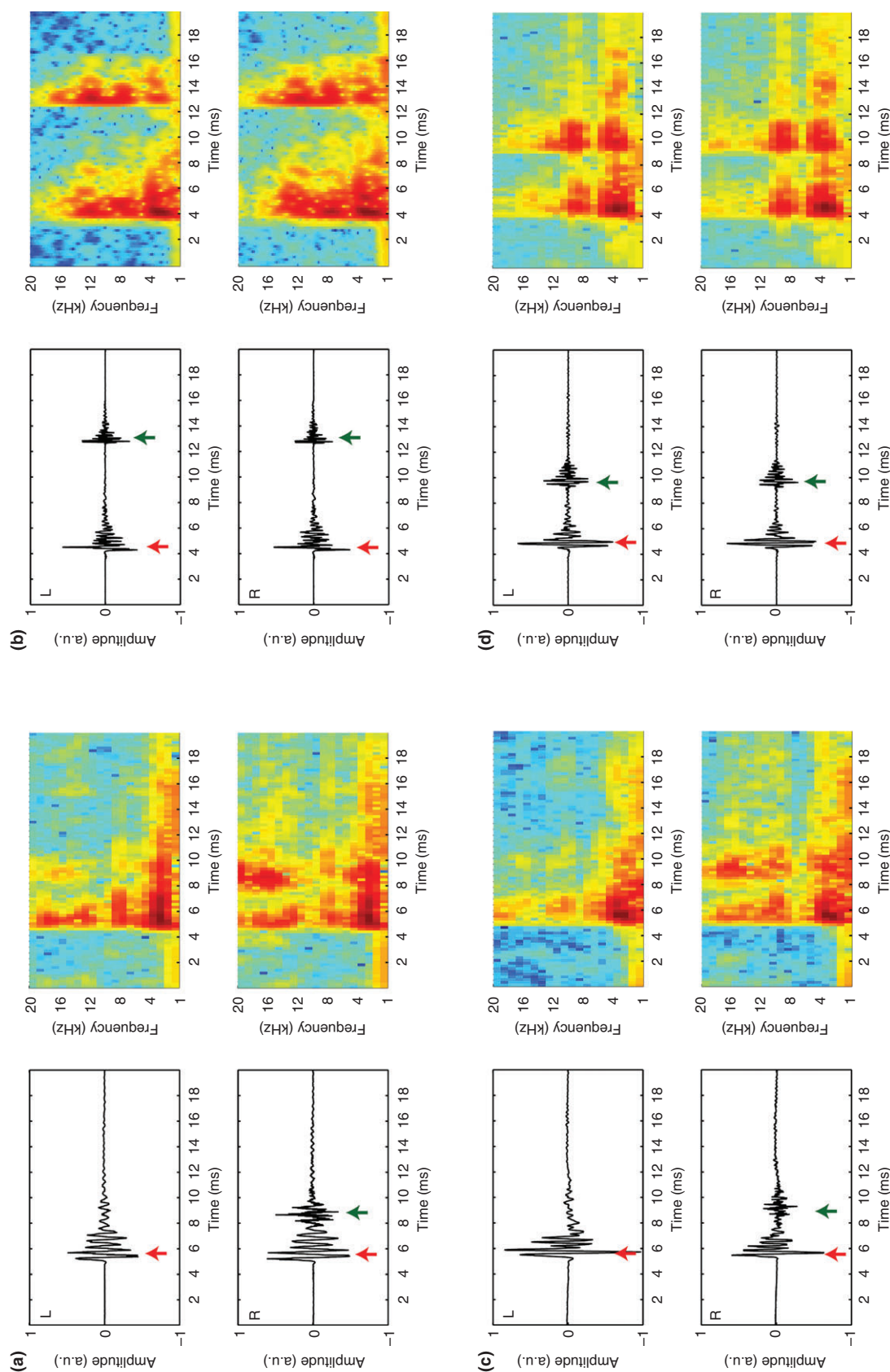


FIGURE 1 | Waveforms, plotting amplitude (a.u. = arbitrary units) against time (ms) and spectrograms denoting frequency (kHz) content as function of time (ms). In spectrograms warmer colors indicate more energy in that frequency band at that moment in time. All figures are based on binaural recordings of clicks and echoes for four different echolocators (a–d). Recordings were made either at the entrance of the echolocators' earcanals (a, c, and d) or next to their ears, that is, on each side of the head, but placed outside the pinna, (b), while they made clicks and listened to echoes. Red arrows in waveform plots highlight clicks, and green arrows highlight echoes. The recording sample frequency was 96 kHz for data shown on the right (b and d), and 44.1 kHz for data on the left (a and c). Spectrograms were calculated using a 1-ms window with 0.8-ms overlap in steps of 1 kHz. For (a) and (c), a sound-reflecting surface was located 60° to their right at a distance of 50 cm. For (b), a sound-reflecting surface was located straight ahead at a distance of 85 cm. For (d), a sound-reflecting surface was located straight ahead at a distance of 150 cm.

in the left ear, while Figure 1(b) and (d) shows that the echoes will be equally strong in the right and left ears when the object is located straight ahead. The figure also shows that if an object is farther away the time delay between click and echo will be longer (e.g. compare Figure 1(b) and (d)). Based on acoustical analysis of the physical properties of various sounds, it has been suggested that mouth clicks might be particularly useful for human echolocation.^{21,22}

HOW GOOD IS ECHOLOCATION FOR DISCRIMINATING LOCATION (AZIMUTH ANGLE), DISTANCE, AND SIZE?

In this section, we review some of the studies that have carried out psychophysical examinations of click-based human echolocation to determine the acuity in perceiving the location (azimuth), distance, and size of sound-reflecting surfaces. Note that in all reports published to date, acuity was measured only in central acoustic space, that is, straight ahead rather than off to the side.

Discriminating Distance

In a recent study,³² it was shown that sighted people using echolocation can, on average, detect a difference of about 40 cm in depth when the surfaces are 170 cm away, 80 cm when they are 340 cm away, and 125 cm when they are 680 cm away (estimates based on Figure 35.1 in Ref 32). These results were obtained using a virtual echolocation paradigm, in which distance was coded in virtual acoustic space by making distance-dependent adjustments in the delay between the emitted sound and the returning echo as well as the drop-off in the intensity of the echo with increasing distance. In a much earlier study by Kellogg¹² that used a real physical setup (a 30-cm wide wooden disk positioned at different distances), a blind individual who used echolocation (Subject C in the experiment) was able to detect a difference of about 10 cm in depth at a distance of 60 cm. Kellogg stated that subjects in his study made use of their voice as well as mouth clicks.

Discriminating Location (Azimuth Angle)

With respect to azimuth, we have found³³ that an individual who had been blind from birth and had learned to echolocate early in life could detect a change as small as 4° in the azimuthal position of a 150-cm tall pole in a two-interval two-alternative forced choice task (i.e., one object was presented at a time and the

person had to determine whether the object had moved to the right or left from one interval to the next) (Figure 1C in Ref 33). With respect to sighted echolocators, it has been reported that they can detect a 6.7° change in the azimuthal position of an 'object' placed 200 cm away.³⁴ These results were obtained using a virtual echolocation paradigm, that is, distance was coded in virtual acoustic space by binaural adjustments of the emission-to-echo delay and the sound intensity. Using a physical setup that measured localization acuity with the echolocation equivalent of a visual vernier acuity task (i.e., subjects had to judge the relative horizontal displacement of two disks presented simultaneously), Teng et al.³⁵ found that blind echolocators were able to detect a difference of around 3.4° when the objects were 50 or 100 cm away. Notably, the best performer had a threshold of 1.22° at 100 cm. Using the same echolocation vernier acuity task with a sample of sighted people, Teng and Whitney³⁶ found the two best sighted performers (i.e., those for which threshold could be computed) were able to detect a difference of 4.1° and 6.7°, respectively, when the objects were 50 cm away.

Discrimination of Size

The acoustic size of an object can be defined as the acoustic angle an object subtends. The acoustic size of an object can be dissociated from its physical size. For example, a smaller object at a closer distance may have the same acoustic size as a larger object farther away. Sighted echolocators, it seems, can detect a change in acoustic size of about 17° and 19° in size for objects located 33 and 50 cm away, respectively, whereas a blind echolocator's threshold at 75 cm was as small as 8° (see Ref 36). These results were obtained using a physical setup in which the participants had to judge the relative sizes of two objects presented simultaneously. We found similar performance in a sighted sample using the same task.³⁷ Importantly, it appears that blind people who are experts in echolocation can discriminate among objects based not only on their 'acoustic size' but also on their real physical size.³⁸ In the visual domain, 'size constancy' is used to refer to the perceptual phenomenon in which objects appear to be the same physical size independent of their 'visual size' (i.e., the visual angle an object subtends on the retina, which changes with viewing distance). The finding that blind people who are experts in echolocation can discriminate among objects based on their physical size (regardless of their 'acoustic size') suggests that size constancy may also operate during echolocation.³⁸

THE NEURAL UNDERPINNINGS OF ECHOLOCATION

The majority of people who are experts in echolocation are blind. In this section, we first review what is known about the neural basis of echolocation, particularly in the blind. We then explore the relationship between blindness and the ability to echolocate.

Neuroimaging of Echolocation

To date, much of the evidence that speaks to the brain mechanisms underlying echolocation in humans has been obtained using neuroimaging, such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). The first study to touch upon the issue of echolocation in people and its underlying neural mechanisms was conducted in 1999 by DeVolder et al.³⁹ Specifically, they used PET to measure activity in blind and sighted people's brains while they were using an echolocation-based sensory substitution device. The device consisted of a pair of spectacles equipped with an ultrasound speaker, two ultrasonic microphones, two earphones, and a processing unit. The device acquired and decoded ultrasonic echoes into audible sounds that were then sent to the user's earphones. The pitch of the audible sounds conveyed distance and the difference in the intensity of the sounds in the two ears conveyed direction. They found that, in the blind subjects, the processing of sound from the device was associated with an increase in brain activity in Brodmann area (BA) 17/18 (i.e., the early 'visual' cortex). Though subjects in the study did not echolocate *per se*, this was first evidence to suggest that the information derived from echolocation may drive early visual cortex in blind people.

Encouraged by these findings, we conducted the first-ever study to measure brain activity during echolocation in two blind people who had learned to use mouth clicks to echolocate.³³ One person lost his sight very early in life and had taught himself how to echolocate. The other person became blind as a young adolescent and was taught to echolocate. Using fMRI, we measured activity in the brain while the two echolocators (and two age-matched sighted controls) listened to sound files that contained clicks and echoes as well as background sounds that had been recorded when the blind echolocators were clicking outdoors in front of different objects. We also measured their brain activity while they listened to sound files that contained both the background noise and the clicks, but no click-echoes (i.e., the echoes had been removed). When we compared the

brain activity associated with listening to the two kinds of sound files, we found that there was significant increase of activity in BA17/18 for the sound files containing the echoes in the brains of the two echolocators but not in the brains of the two sighted controls. Figure 2 illustrates the results in the person who lost his sight very early in life and an age and gender-matched sighted control participant.

In this and subsequent studies,⁴⁰ we found that echo-related activity in BA17 in each hemisphere was stronger for echoes coming from contralateral space (i.e., for echoes coming back from objects located in the side of space contralateral to the hemisphere), and that the pattern of activity changed in a reliable way as the echoes move away from the centre toward the periphery of space (i.e., there was modulation of activity with eccentricity). A recent fMRI study⁴¹ has since replicated the involvement of BA17 in echolocation in the blind.

Since this initial work, we have gone on to investigate the neural substrates of human echolocation in more detail. We have shown that 'echo-acoustic motion' (echoes coming back from moving objects) activates brain areas in temporal occipital cortex, close to, or possibly coinciding with visual motion area MT+ in sighted people.⁴² Activations for echolocation motion in these brain areas in our blind participants again showed a contralateral preference. Most interestingly, in the same study we also compared the processing of source-sound motion in processing of echolocation motion, and found that even though both types of acoustic motion activate adjacent areas in temporal occipital cortex, the activations for the two types of motion appear to form functionally distinct clusters in both blind and sighted people (Figure 4 in Ref 42).

In another study⁴⁰ we found that echoes coming back from surfaces with different shapes (concave versus convex, for example) tend to differentially activate the lateral occipital complex in the brain of blind echolocators, a ventral-stream brain area that has been implicated in the visual processing of shape in the sighted brain. In another study⁴³, we also found that echoes coming back from surfaces made of different materials (e.g., fleece, whiteboard, foliage) tend to differentially activate a region in left parahippocampal cortex (PHC) in the brains of blind echolocators, and this may correspond to the same general regions of PHC that have been implicated in both visual and auditory processing of material properties in the sighted brain.^{44–46} We also have found that both blind and sighted people show activation in posterior parietal cortex during echolocation of path direction for walking,⁴⁷ and the location of this

activation might coincide with dorsal-stream areas involved in processing of vision for motor action.⁴⁸

In support of the idea that echolocation may have links to visual processing it should also be mentioned that there is evidence of direct anatomical connections between primary auditory and visual cortices in primates.^{49,50} Nonetheless, even though the existence of such connections may explain how acoustic stimuli may feed into visual processing areas, it would not explain why echolocation should play a different role, for example, as compared to source sounds (e.g., see Ref 42).

In sum, although there are only few studies to date that have explored the neural substrates of natural echolocation, it would appear that there is converging evidence for the idea that traditional 'visual' brain areas are involved during echolocation in blind echolocation experts, and that this activation appears to be feature (and task) specific.

Echolocation and Blindness

The literature to date suggests that blind people are more sensitive to acoustic reverberations than sighted people even when they do not consciously echolocate. For example, it has been shown that blind people have a better ability than sighted people to

resolve two 2500 Hz sounds occurring in rapid succession.⁵¹ In other words, a blind person might be able to hear two sounds rather than one when the two sounds are separated by a silent gap as short as 5 ms. In contrast, a sighted person may hear only a single merged sound (Table 2 in Ref 51). This ability might contribute to blind people's ability to resolve small differences in the arrival time of echoes. A possibly related phenomenon is the fact that blind, as compared to sighted, people show a reduced latency in component V of the auditory brain stem response to a click stimulus.⁵² Specifically, component V appears only 5.5 ms after stimulus onset in blind people, but takes 5.8 ms in sighted people (Table 1 in Ref 52).

It seems likely that blind people's increased sensitivity to echoes can be an advantage when the goal is to process those echoes. In fact, blind people who are not specifically trained in echolocation are better at determining whether a sound reflecting surface is located on the right or left side of space than sighted people.⁵³ There is also the question of distance. When judging the distance of a sound, one can make use of the direct to reverberant ratio (i.e., the relative intensity of the direct sound over the relative intensity of the reverberant sound from surrounding surfaces). The further a sound is positioned away from a

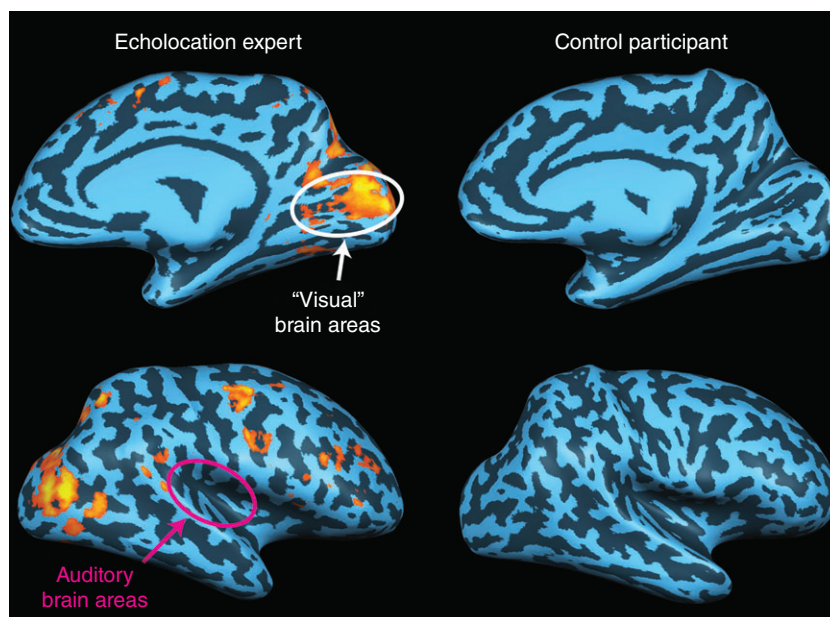


FIGURE 2 | Illustration of results from Ref 33. For the echolocation expert who had lost vision very early in life (left side panels) areas highlighted in warm colors show an increase in BOLD signal when the participant listened to sound containing background sounds, clicks and echoes as compared to sounds that contained background sounds and clicks, but no echoes. The echolocation expert shows a relative increase in 'visual' cortex, including BA17/18. Interestingly, for the same contrast we did not observe an increase in activity in early auditory areas (i.e., Heschl's gyrus and surround). For the age- and gender-matched sighted control participant we did not observe any increase in BOLD for the same contrast.

listener the smaller this ratio. As it turns out, blind people are better at using this information than sighted people, revealing (again) higher sensitivity to sound echoes.^{54,55} Interestingly, this increased sensitivity to echoes is also present when the best strategy would be to ignore echoes. Indeed, Dufour et al. found that irrelevant echoes bias blind listeners' judgments about the location of a surface more than sighted listeners' judgments.⁵³

Importantly, there are also differences among people who are blind. For example, we have shown that blind people who have been trained to be skilled in echolocation are better at determining the shape, size, or distance of objects on the basis of echoes than are both blind and sighted people who have no expertise in echolocation.^{29,38,43,47} Furthermore, a positive correlation between echolocation ability and the age of the onset of blindness has been found, showing that people who lost vision earlier in life tend to be better at echolocation compared to people who lost their vision at a later age.³⁵

On the behavioral level, researchers have shown that echolocation may be more than a simple 'substitute' for vision, but actually share some of its features. In one recent study⁵⁶, it was shown that blind people trained in echolocation (but not blind people untrained in echolocation) experienced a 'size-weight illusion' when they used echolocation to get a sense of how big objects were, and then judged their weight. In other words, like sighted people, they judged the smaller object of two objects to be heavier than the larger one, even though the two objects weighed exactly the same. In addition, it has been shown that when people are asked to judge the relative locations of two sounds (using a spatial bisection task), blind people who are not trained in echolocation show a deficit in this task compared with sighted people.^{57,58} In contrast, blind echolocators perform equivalent to sighted people.⁵⁸ This shows that echolocation may replace vision for the calibration of external auditory space in people who are blind.

These results, in combination with findings from brain imaging, suggest that echolocation may fulfill the same role within human perception as vision, particularly in the blind.

ECHOLOCATION AND CROSS-MODAL PLASTICITY

As outlined above, there is converging evidence for the idea that traditional 'visual' brain areas are engaged when blind echolocation experts are listening to their own clicks and echoes. Similar appropriation of visual brain areas has been reported in other

modalities. For example, 'visual' cortex activation has been observed for tactile and auditory processing after both long- and short-term visual deprivation (for reviews see Ref^{59–64}). In fact, in the last 15 years, scientists from a variety of disciplines have gained considerable insight into sensory abilities and brain reorganization in blind and sighted people following the use of visual-to-auditory or visual-to-tactile sensory substitution devices.⁶⁵ It has also been suggested that early 'visual' areas in blind people are commandeered for interpreting Braille⁶⁶ or processing spoken language.⁶⁷

In sum, blindness can lead to considerable reorganization of occipital brain areas and for this reason, it is perhaps not surprising that the use of echolocation by blind people might lead to measurable increases in activation in traditional 'visual' areas. At the same time, the fact that there is a strong link between echolocation and visual abilities, such as the calibration of acoustic space⁵⁸ and contralateral preference for the processing of echoes,^{33,42} suggests that the innate spatial organization of visual cortex may pre-dispose it for being co-opted for echolocation, which by its very nature is spatial as well. It would be informative to compare the changes that occur in occipital cortex in response to the acquisition of echolocation in blind people, with the changes in these same regions of cortex that have been linked to tactile processing and the processing of source sounds.

Finally, there may be parallels in the changes that occur in the brain when other sensory modalities are lost. For example, there is evidence that congenitally deaf animals and humans show activity in auditory cortex when they are engaged in different visual tasks^{59,68,69} and that this activity can support certain visual functions.⁷⁰ An examination of the differences and similarities in the way different brain areas are recruited in the blind and deaf brain could uncover some general principles underlying neuroplasticity when an important sensory channel is compromised.

ECHOLOCATION, SPECIALIZATION AND VISION—COMPARISON TO BATS

Echolocation abilities in bats are the result of millions of years of evolution,^{71,72} whereas the ability of a blind person to echolocate is established during a single lifetime. Bats exhibit distinct specializations for echolocation, such as specifically formed organs to emit sonar emissions, a movable outer ear, as well as neural specialization within their auditory brain stem

and cortex⁷³ such as delay-tuned neurons^{74,75} and expansion of neural representation around ‘echo expected’ frequencies.⁷⁶ To date, such specialization has not been observed in human echolocators. Rather, as pointed out above, echolocation is more likely to co-opt existing auditory and visual pathways and mechanisms. Yet, we are just beginning to understand how the human brain deals with information provided by echolocation and more research is needed to work out how echolocation is integrated into the human perceptual systems.

For echolocating bats, it has been suggested that echolocation and vision are used in parallel and that they may provide complementary ways of dealing with different aspects of their environment. For example, echolocation might be more useful for detecting and hunting small prey, while vision might be more useful for large scale navigation and orientation.⁷⁷ This ‘division of labour’ has been suggested based on analysis of bat echolocation and visual abilities, and the estimated perceptual information gain under various scenarios.

Yet, a ‘division of labour’ between vision and echolocation might not apply in the human perceptual system. Specifically, the behavioral evidence currently suggests that the spatial resolution of human, as compared to bat echolocation, is much more limited. This is not surprising given the fact that most bats use ultrasound for echolocation whereas humans use sounds in the audible range. Furthermore, the human visual system provides great spatial detail across many conditions and scenarios. Thus, one would expect only limited perceptual gains for echolocation in sighted individuals—although clearly echolocation would have an advantage in the dark. In the blind, however, echolocation can provide considerable perceptual gains—particularly when combined with the use of the cane. Thus, even though a division of labor between vision and echolocation might apply in bats, it is less likely to be the case in humans. Rather, in people who are sighted, vision is likely to take general precedence over echolocation, while in people who are blind, echolocation may serve as vision substitute.

In sum, even though the same physical echolocation principles apply across bats and humans the purpose that echolocation fulfills may not necessarily be the same across species. Bat echolocation systems have evolved over a long time and bats show behavioral, anatomical, and neural specializations not necessarily observable in people. Thus, even though findings from bat echolocation research can serve as starting point for investigations in people (or vice versa), findings may not necessarily generalize from

one species to the other so that additional investigations are necessary.

APPLICATIONS

People who are blind and echolocate show a high level of independence in their daily life. Indeed, in a recent survey⁷⁸ we found that blind people who use echolocation report better mobility in unfamiliar places and also earn higher salaries than blind people who do not echolocate. This implies that the use of echolocation in blind people is not only associated with perceptual benefits as measured in the lab (e.g., see the psychophysical literature reviewed in previous sections) but also with functional benefits in daily life.

To date echolocation is not part of the mobility curriculum in institutions and organizations who work with the blind. This is supported by the fact that most people are self-taught or they obtain training through their own initiative. It is possible that sonar emissions such as mouth clicks that are often used by blind echolocators are regarded as potential stigma. But this ignores the fact that in our experience blind people who use echolocation are sensitive to the social situation that they are in—and modulate their clicks or other sonar emissions accordingly. Another possibility for the low use of echolocation by people who are blind is that use of echolocation is discouraged by sighted people who do not know the function of the process. For example, various echolocators we know have a story to tell about being forbidden to use echolocation by teachers or social workers, mostly with the argument that it is not an appropriate behavior. These comments may be due to the educators’ poor knowledge of echolocation. All people who we know who use echolocation also use the long cane and/or a guide dog, or a human guide (particularly in the case of blind individuals using a wheelchair). This observation is also supported by survey results in Ref 78. The reason that blind people combine echolocation with other mobility tools is because of the obvious benefits of echolocation in detecting and localizing obstacles at head height and in way-finding and orientation, even though it is less useful for detecting obstacles on the ground (which is why they also use a cane or a guide dog). Importantly, as mentioned earlier, echolocation may not only be useful for day-to-day mobility,⁷⁸ but its use may also offer more broad cognitive benefits, such as the general representation of space. For example, people who are totally blind from an early age tend to have deficits in representing spatial

relationships between objects or the spatial structure of a scene.⁷⁹ This can, for example, present as a deficit in determining the spatial relations among multiple source sounds, for example, determining whether a sound originates from a location in space that is closer or further away with respect to a sound presented in a previous location.⁵⁷ Most notably, people who have been blind from birth, but who use echolocation, appear to understand these spatial relationships significantly better than people who have been blind from birth and who do not use echolocation, and equally well as sighted people.⁵⁸ Thus, there is the possibility that echolocation may substitute for vision in calibrating spatial layout of sounds in people who are blind. In sum, based on our current knowledge, we would suggest that educators, social workers, and policy makers should encourage and facilitate the use of echolocation alongside the use of other mobility methods.

Over the years various technological assistive devices for people with vision impairments have been developed based on the echolocation principle.^{80–89} Some of these devices are distance measures or localization devices; that is, these devices send out an ultrasonic pulse and then transform the incoming information into a secondary signal about distance and location, which is then fed back to the user. Other devices, such as those described in Ref 88, are based on the idea that the signal should not be changed but that the user's brain 'should do the work'. These devices send out an ultrasonic emission, and receive the echoes binaurally via artificial pinnae, and then simply down-sample the signal and send the down-sampled (but otherwise 'raw') signal to the user via headphones. In this way, it is up to the user to extract the relevant information from the signal.

The advantage of technological assistive devices is that in principle they can, for example, achieve greater resolution by working in the ultrasonic range. All devices we are aware of are developed for and worn by adults, even though the sonic guide in particular^{84–86} was provided with a training manual specifically for children, and its successful use has also been documented in blind children, with the usage of the device starting in babies as young as 2-weeks old.⁹⁰ The fact that a device may not have been made specifically for children, does of course not exclude its use by children. Yet, certain adaptations may have to be made to make them child-friendly (i.e., size, weight, sturdiness). Even though early adoption of an assistive device is more likely to lead to successful development of the skill, such intervention will fail if the device is not usable by children or prevents them from engaging in their day-to-day

activities. Natural echolocation has several clear advantages: it does not need batteries, it is cheap, it cannot be forgotten at home, it does not break—and importantly, it can be learned by children (for more information see www.worldaccessfortheblind.org/). Moreover, making mouth clicks does not interfere with other activities (i.e., they can be modulated and even stopped when the person wants to talk or do something else).

In sum, even though assistive technology can in principle offer greater spatial resolution, natural echolocation offers advantages in terms of ease of access, sturdiness, and low cost. Of course, it is also possible to combine the two. In our opinion, the reason that neither natural echolocation nor echolocation based assistive technology are widely used at present is most likely a combination of lack of knowledge of benefits of echolocation, a lack of integration in mobility curricula, and little attention to the requirements of the user in device development (i.e., devices are developed by researchers and users are subsequently 'taught' to use the device, instead of starting from the perspective of the user to begin with).

In this section, we have addressed the implications of echolocation for mobility and orientation and a potential general cognitive benefit for people who are blind. This is clearly a major putative function of human echolocation and for this reason it is critical that we better understand how it works. At present, laboratory and applied 'real-life' echolocation remain distressingly unconnected. There is also a relative paucity of empirical data on the real-life benefits of echolocation, both as direct perceptual aid and potential cognitive enhancement. In our opinion the gap between perceptual research and applied mobility should be bridged by conducting research in these domains in parallel.

OUTLOOK—BEYOND ECHOLOCATION AS A NICHE RESEARCH AREA

To date, most of the research into echolocation has relied on the comparison between blind echolocation experts and blind and sighted control participants. One of the drawbacks of the research is that echolocation experts are quite rare (at present), and thus sample sizes are small. Even though statistical methods are at hand to deal with these challenges, there is still the problem that the level of expertise in echolocation tends to be confounded with the amount of visual experience that an individual might have had. Moreover, many of the people who have been

studied were self-taught. All of this gives the research something of a 'niche' character. But teaching individuals, blind and sighted, to echolocate at different ages and under different conditions opens unique possibilities here. Not only does it provide control over the amount of visual deprivation and the role that might play in acquiring the ability to echolocate, but it also provides a powerful paradigm to investigate how the brain learns to deal

with new information. Furthermore, because echolocation is an active process and each click is designed to acquire a sensory 'sample' and thus can be tracked, it opens a powerful window for investigating the principles of sensory processing. In this way, then, echolocation cannot only be investigated in its own right, but it can be used as a tool to investigate neuroplasticity and information processing on a more general level.

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