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## Seeing with sound: Investigating the behavioural applications and neural correlates of human echolocation

Jennifer L. Milne  
*The University of Western Ontario*

Supervisor  
Dr. Melvyn A. Goodale  
*The University of Western Ontario*

Graduate Program in Neuroscience  
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of  
Philosophy  
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SEEING WITH SOUND: INVESTIGATING THE BEHAVIOURAL  
APPLICATIONS AND NEURAL CORRELATES OF HUMAN ECHOLOCATION

(Thesis format: Integrated Article)

by

Jennifer L. Milne

Graduate Program in Neuroscience

A thesis submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy

The School of Graduate and Postdoctoral Studies  
The University of Western Ontario  
London, Ontario, Canada

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## Abstract

Some blind humans use the reflected echoes from self-produced signals to perceive their silent surroundings. Although the use of echolocation is well documented in animals such as bats and dolphins, comparatively little is known about human echolocation. The overarching goal of the work presented in this thesis was to shed light on some of the basic functions of human echolocation, including the perception of the shape, size, and material. I addressed these aspects of echolocation using behavioural psychophysics and neuroimaging.

In Chapter 2 I show that blind echolocators were able to accurately identify the shape of 2D objects, but that their ability to do so was dependent on the use of head and body movements to ‘scan’ the objects’ edges. I suggest that these scanning movements may be similar to the many saccades made by sighted individuals when visually surveying an object or scene.

In Chapter 3 I addressed the possibility that object size perception via echolocation shows size constancy – a perceptual phenomenon associated with vision. The results revealed that an expert echocator accurately perceived the true physical size of objects independent of their distance, even though changes to distance directly affect size-related echo information. The results of this study highlight the ‘visual’ nature of echolocation, and suggest further parallels between the two modalities than previously known or theorized.

Chapter 4 presents the results of a functional neuroimaging study aimed at uncovering the neural correlates of material processing via echolocation. By having echolocators listen to recordings of echoes reflected from surfaces of different materials, I show not only that they can determine the material properties of objects, but also that the neural processing underlying this ability may make use of a visual- and auditory-material processing area in the parahippocampal cortex.

Taken together, the work presented in the current thesis describes some of the recent contributions to our understanding of human echolocation, with a particular emphasis on its apparent parallels with vision and visual processing.

The results of this work show that accurate and reliable information can be extracted from echoes, thus supporting echolocation as a viable resource for the blind.

## Keywords

Human echolocation, echo, blindness, neuroplasticity, multisensory, vision, audition, shape, size constancy, material properties, fMRI

## Co-Authorship Statement

All of the studies contained within this doctoral thesis dissertation were conducted in collaboration with my supervisors, Dr. Melvyn A. Goodale and Dr. Lore Thaler. While not listed as an official author, Caitlin Byrne assisted with data collection for the projects contained in Chapters 2 and 3. Mimma Anello assisted with the experimental design, data collection, and analysis of the work contained in Chapter 3. The written material in this thesis is my own work, but, as my supervisors, Dr. Goodale and Dr. Thaler provided assistance in editing and revising all of the material contained within this thesis.

At the time of publication of this thesis, Chapter 2 has been published in *Attention, Perception, & Psychophysics*, Chapter 3 has been published in *Neurocase*, and Chapter 4 has been accepted pending revisions in *Vision Research*.

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Milne, J.L., Anello, M. Goodale, M.A., & Thaler, L. A blind human expert echolocator shows size constancy for objects perceived by echoes. *Neurocase*, doi:10.1080/13554794.2014.922994.

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I would also like to thank Lore Thaler, my co-supervisor. As a former post-doc of Mel's, Lore was the first in the lab to study human echolocation. I am so thankful that she and Mel asked me to be a part of the echolocation research – it has been an incredible and unique experience. Lore has helped me to become a critical and careful thinker, and her thorough and helpful feedback has improved my writing tremendously. I cannot thank her enough for her help and guidance in preparing this dissertation and all of the projects contained within it.

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## List of Abbreviations

**2D:** Two-dimensional  
**ANOVA:** Analysis of variance  
**BA:** Brodmann area  
**BC:** Blind non-echolocating control participant  
**BOLD:** Blood oxygenation level dependent  
**CF:** Constant frequency  
**CI:** Confidence interval  
**CoS:** Collateral sulcus  
**dB:** Decibel  
**EE:** Expert echolocator  
**FDR:** False discovery rate  
**FM:** Frequency modulated  
**fMRI:** Functional magnetic resonance imaging  
**GLM:** General linear model  
**Hz:** Hertz  
**ILD:** Interaural level difference  
**ITD:** Interaural time difference  
**LOC:** Lateral occipital complex  
**MGN:** Medial geniculate nucleus  
**MT+:** visual-motion area  
**MVPA:** Multi-voxel pattern analysis  
**PET:** Positron emission tomography  
**PHC:** Parahippocampal cortex  
**RMS:** Root mean square  
**SC:** Sighted blindfolded control participant  
**SD:** Standard deviation  
**SEM:** Standard error of the mean  
**SSD:** Sensory substitution device  
**TMS:** Transcranial magnetic stimulation



Chapter 1:  
General Introduction

## 1.1 Why Study Human Echolocation?

Human echolocation refers to the ability of some blind humans to use the echoes from self-generated auditory signals to perceive silent objects and surfaces in their environment. For example, by producing a clicking sound with their mouths, expert echolocators can then listen for reflected echoes, which contain information about the size, shape, location, distance, motion, and material properties of objects (for reviews, see Stoffregen & Pittinger, 1995; Kolarik, Cirstea, Pardhan, & Moore, 2014). The use of echolocation, then, can provide blind individuals with a rich source of information that has obvious implications for navigation and obstacle avoidance; furthermore, the enriched perceptual experience echolocation affords these individuals is not trivial. Despite the clear benefits and advantages that echolocation can offer the blind community, very little research has been dedicated to understanding echo perception in blind humans.

In the absence of vision, the perception of one's surroundings is achieved with the remaining senses. Specifically, a blind individual can explore and identify objects haptically (i.e. via touch) and can also localize and identify objects based on the sounds they emit. But how would a blind individual perceive objects that are silent and beyond reachable space? Without vision, the perception of objects in such a situation would be impossible. The use of echolocation, though, offers the opportunity for blind individuals to overcome this issue, as the use of echoes allows individuals to perceive silent objects at a distance. Therefore, echolocation can serve to a degree as a substitute for vision because it allows blind individuals to perceive aspects of their environment that are not directly accessible via any of the remaining senses.

It is a rare opportunity in science to encounter a topic area that is both exceptionally interesting and relatively untapped in terms of empirical research. Although there have been anecdotal reports on enhanced sensory abilities of the blind in past centuries and also some behavioural investigations during the mid-20th century, research in the field has failed to gain any significant traction. It has been only recently that human echolocation has captured the attention of a small

number of researchers, and our understanding of the use of echolocation techniques by blind humans is now only slowly developing. Given the obvious benefits of echolocation, it is important to continue to better our understanding of the technique in order to validate its utility as an additional resource for the blind. The current thesis explores some of the behavioural applications of echolocation as well as the neural underpinnings of echo processing, all with the 'visual' nature of echolocation in mind.

## 1.2 Sensory Loss

Before delving into the literature on echolocation, it is important to have a basic understanding of how the absence of vision affects the structure and function of the brain. Humans are undoubtedly visual animals, and we rely heavily on vision for perceiving and acting within our environment. This is reflected in the substantial amount of cortex dedicated to the processing of vision and its related functions. Furthermore, it has been argued that it is vision that is the dominant sense, and that visual input is required for calibrating certain aspects of audition and somatosensation (Rauschecker, 1995; in animals: Brainard & Knudsen, 1998; Knudsen, 1998). But, if the human brain is so reliant on visual information, what happens in the absence of this input? There is a common belief that, in the absence of one sensory system, the remaining sensory systems become enhanced to compensate for the loss. While this is certainly a generalized and over-simplified statement, there is an element of truth to it. It is not uncommon for other neural processes to extend and strengthen connections into the available 'real estate' in the brain; that is, the cortical areas normally dedicated to the processing of the sense that is absent. This process – known as neuroplasticity – is actually a feature of the healthy brain and is the mechanism for learning, growth, and development (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). Since the brain is the source of human behaviour, it must be capable of being molded by environmental pressures, physiological modifications, and experience. This applies especially in cases where sensory input is absent, and the brain

often compensates for the lack of input by increasing the cortical representation of one or more of the remaining senses.

### 1.2.1 Behavioural Sensory Compensation

As discussed above, the absence of sensory input from a particular modality may result in behavioural compensation in one or more of the remaining senses. In the case of blindness, superior performance (compared to sighted individuals) has been observed in both the somatosensory (i.e. tactile) and auditory domains. For example, several studies have shown that blind individuals are superior to sighted individuals in discriminating grating orientation with their fingertips (Goldreich & Kanics, 2003; Legge, Madison, Vaughn, Cheong, & Miller, 2008; Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000). Furthermore, it was found that these tactile improvements did not correlate with Braille-reading proficiency or the age at which the individuals learned to read Braille (Legge et al.). It remains unclear, though, whether the enhanced tactile sensitivity is due to the lack of visual input *per se*, or to the fact that blind individuals rely more heavily on tactile cues (e.g., for Braille reading and object exploration). There is evidence to suggest that the increased sensitivity is simply due to experience with Braille reading, with results indicating that the reading finger on the dominant hand shows the most improved sensitivity (although the non-reading fingers on the dominant hand showed some improvement as well) and no sensitivity differences from sighted individuals for tactile stimulation of the lips (Wong, Gnanakumaran, & Goldreich, 2011). However, Chebat, Rainville, Kupers, and Ptito (2007) saw improvements in sensitivity on the tongue in a subset of their blind participants, thus suggesting that widespread and nonspecific somatosensory enhancement may occur in at least some blind individuals.

The possibility of auditory sensitivity enhancement in the blind, on the other hand, has been tested more thoroughly. For example, numerous studies have shown that blind individuals show enhanced pitch – or frequency – perception. More specifically, blind individuals are better than sighted individuals at discriminating the pitch of sounds (Wan, Wood, Reutens, & Wilson, 2010), and

they can also perceive changes in pitch at speeds as much as ten times faster than sighted people (Gougoux et al., 2004). Furthermore, the prevalence of perfect pitch – that is, the rare ability to specifically identify the pitch of tones without a reference – is significantly higher in blind individuals with musical training as compared to sighted musicians (Hamilton, Pascual-Leone, & Schlaug, 2004). Blind people also have better auditory temporal resolution (Muchnik, Efrati, Nemeth, Malin, & Hildesheimer, 1991).

Perhaps the most widely studied aspect of auditory compensation in the blind is in sound localization. Blind participants have been shown to have binaural auditory spatial mapping that is comparable or superior to sighted individuals; furthermore, blind participants show enhanced monaural localization as compared to sighted listeners (Lessard, Paré, Lepore, & Lassonde, 1998). Further investigations on auditory localization have revealed that the enhancement seen in blind individuals is typically in the peripheral auditory fields only (Röder et al., 1999). In addition, blind individuals show superior performance to sighted individuals in discriminating the distance of sound sources using direct-to-reverberant cues (Kolarik, Cirstea, & Pardhan, 2013). These findings suggest that, although vision may normally dominate in calibrating spatial relations, the absence of visual input – particularly during development – may allow for auditory spatial relationships to become more developed and refined in an atypical fashion. On the other hand, visual calibration may play an important role in forming Euclidean auditory relationships because blind individuals show a deficit on more difficult auditory tasks, such as the spatial bisection of source sounds (Gori, Sandini, Martinoli, & Burr, 2014) and localization along the vertical plane (Zwiers, Van Opstal, & Cruysberg, 2001). Overall, the existing evidence suggests that blind individuals do show enhanced auditory abilities, but these enhancements may manifest differently across individuals and may be beneficial for only certain classes of auditory tasks.

### 1.2.2 Neural Reorganization Following Sensory Loss

For blind individuals to show behavioural improvements in auditory and tactile tasks there must be changes at the cortical level that underlie and produce these enhancements. Numerous studies have shown that the occipital cortex of blind subjects is activated during auditory and tactile tasks (for review, see Collignon, Voss, Lassonde, & Lepore, 2009). For example, a positron emission tomography (PET) study found that the occipital cortices of the blind participants but not the sighted participants were activated during an auditory localization task (Weeks et al., 2000). A separate PET study showed that during a monaural sound localization task (on which blind individuals typically outperform sighted individuals, as discussed above) blind participants showed activation in the occipital cortex, and this was not seen in sighted participants (in fact, during a binaural task sighted participants actually showed a decrease in activity in the occipital cortex) (Gougoux, Zatorre, Lassonde, Voss, & Lepore, 2005). Furthermore, the activity in the occipital cortex of the blind participants was strongly correlated with their sound localization accuracy. In addition to general sound-related activation in the occipital cortex, evidence suggests that there is feature-specific activation. More specifically, the use of a sensory substitution device that converts visual shape information into auditory shape signals was found to activate the lateral occipital complex, an area traditionally associated with the processing of visual shape and form (Amedi et al., 2007).

While the findings discussed above are certainly intriguing and suggest a relationship between behavioural and functional compensation, causal links are necessary in order to draw such a conclusion. Collignon, Davare, Olivier, and De Volder (2009) specifically addressed causality by applying transcranial magnetic stimulation (TMS) to the brains of blind participants while they performed a sound lateralization task. When TMS was applied to the intra-parietal sulcus (a brain area in sighted individuals that is critical for the spatial processing of sound), the researchers saw no change in performance on the task. When TMS was applied to the occipital cortex, however, the participants' performance was disrupted.

These results suggest that the occipital cortex of early-blind individuals can reorganize to support auditory spatial processing.

A particularly interesting case related to tactile processing in the blind also sheds light on causality between behavioural and functional compensation. Specifically, following a bilateral occipital stroke, a blind woman was no longer able to interpret Braille, although she had been a proficient Braille reader prior to her stroke (Hamilton, Keenan, Catala, & Pascual-Leone, 2000). Interestingly, her somatosensory perception of the Braille was intact – that is, she could detect the Braille and feel the spatial relationships of the bumps. What she could not do, however, was infer the meaning of the Braille. This suggested, then, that the occipital activation typically seen in Braille readers (Burton et al., 2002; Sadato et al., 1996) likely underlies the understanding but not the sensation of Braille. Supporting this possibility is a TMS study that applied short bursts to the occipital cortex during Braille reading to disrupt processing in that area. They found that blind individuals showed an increased number of interpretation errors when TMS was applied to occipital areas but not to a control area (Cohen et al., 1997). Overall, these studies suggest that in the absence of visual input the occipital cortex not only plays a special role in the interpretation of Braille, but also that increased or strengthened connections between somatosensory and occipital cortices must exist to mediate the two components of Braille reading (i.e. tactile and interpretation).

### 1.3 Echolocation in Animals

Echolocation is a rare practice among animals, and the use of echo perception is typically limited to animals whose living environments are not conducive to the use of vision (for example, nocturnal, deep-sea, and in-ground-dwelling animals). Of all mammals, bats and the Cetacea (whales and dolphins) have the most advanced echolocation capabilities, although some other small insectivores (for example, shrews) use echolocation on a more basic level (Altringham, 1996). In addition, there are some species of birds that echolocate at least to some extent; for example, cave dwelling birds such as the South American oilbird and the

South-East Asian swiftlets (Brinklov, Fenton, & Ratcliffe, 2013; Price, Johnson, & Clayton, 2004). Because the most extensive amount of research has been conducted on echolocating bat species, the remainder of this section will focus primarily on an overview of the current knowledge regarding bat echolocation.

### 1.3.1 Bat Echolocation : An Overview

The first experiments on the navigation and location methods of bats were performed in 1793 by Lazzaro Spallanzani, who discovered that bats were able to navigate with their eyes covered and in total darkness (Griffin, 1959). Although the bats did not appear to use their eyes very much, Spallanzani found that covering or damaging their ears proved to be detrimental and the bats would collide with obstacles and were unable to hunt successfully. At that time, though, it was thought that bats were mute and it was not until some 130 years later that ultrasonic detection technology was created and it was discovered that bats had the ability to avoid obstacles using sound. Finally, in 1938 Griffin demonstrated that bats emit sounds in the ultrasonic frequency range and listen to echoes from objects in the path of the sound beam, allowing them to orient and locate objects in the dark. It was Griffin who coined the term 'echolocation' (Griffin 1944; 1958).

Echolocation is similar to other sonar systems (for example, radar) in that the animal utilizes reflected echoes from self-produced sounds. Bats typically use one of two high-frequency call styles: a constant frequency (CF) call or a frequency modulated (FM) call (Suga & O'Neill, 1979). Some species of bats also use a combination of CF and FM calls. CF calls, as their name suggests, are of a single frequency to which the bat's auditory system is specifically tuned and are usually of a longer duration (10 – 50+ ms). For the most part, CF calls (or the CF component of CF-FM calls) are useful for the simple detection of objects, regardless of any object features, such as size, shape, and material. Because CF calls are of a single frequency, they are also useful in determining the relative velocity of objects (for example, a flying insect) toward or away from the bat (Simmons, Howell, & Suga, 1975). This is due to Doppler shift, which refers to the changes in the frequency of the echoes as an echo-reflecting surface moves



toward (increase in frequency) or away from (decrease in frequency) the bat. Bats that use CF calls show neural specialization for processing sound at and around their call frequency. These bats can modulate the frequency of their calls – for example, to compensate for Doppler shift – so that the resulting echo occurs at the preferred frequency.

FM calls, on the other hand, are typically shorter in duration (0.5 – 10 ms) and rapidly sweep across a wide range of frequencies (i.e. they are broadband signals). Because FM calls are broadband, this makes them particularly suitable for gathering information about object features, such as size, shape, material properties, and distance, because the frequency components of the signal (and the intensity at each of the components) can be compared to those that are present in the echo. For example, the size of objects can be determined via overall echo intensity (i.e. larger objects will reflect a greater amount of signal than smaller objects) and also through the object aperture (that is, the spread of angles from which the echoes are reflected) (Heinrich et al., 2011). Similarly, shape information can be inferred from the intensity of the echo as well as spectral differences in the echo (relative to the signal). In terms of material perception, the broadband FM call is especially useful, because reflective materials tend to reflect sound across the entire range of frequencies while absorptive materials tend to absorb high frequencies and reflect only lower frequencies (Simmons, Howell, & Suga, 1975).

In terms of distance perception, echolocating bats can determine the distance of a target object by listening for the delay between their own sound production and any returning echoes (Jones, 2005). In fact, neurons in the auditory cortex of echolocating bats are specifically tuned to these delays (Wenstrup & Portfors, 2011; Köss, 2014). Differences in echo intensity and the time of arrival of the echoes at the ears are cues used to determine location (particularly in terms of horizontal angle) (Muller, 2004).

The above discussion is a simplification of the mechanisms used for extracting and interpreting echo information, but at a basic level these processes aid the bat in navigating its environment and hunting for prey. These basic

principles also apply to human echolocation, and they will be discussed within this context in the following sections.

## 1.4 Echolocation in Humans

### 1.4.1 The Palatal Click

Although any acoustic signal can theoretically be used for echolocation, the palatal click – or mouth click – is by far the preferred signal of expert echolocators. The clicking sound is produced by rapidly moving the tongue backwards and downwards from the hard palate directly behind the teeth. The signals produced in this way tend to be short and spectrally broad, and are thus quite similar to the FM calls used by some species of echolocating bats (although they are at lower frequencies due to the smaller human audible range). Although expert echolocators typically use the palatal click, they also report using other signals such as finger-snaps, hand claps, tapping of the white cane, and vocalizations other than mouth-clicks. Given the number of possibilities for producing a signal, researchers have aimed to determine the best type of signal to use, but a consensus is lacking. For example, it has been suggested that longer-duration signals (500 ms) may be better than shorter ones because they result in a surplus of echo information due to repetition pitch (Schenkman & Nilsson, 2010). Also, some say that noise signals provide more and better information than click signals (Arias & Ramos, 1997), though it has also been suggested that in particular the palatal tongue click is the best signal for echolocation (Rojas, Hermosilla, Montero, & Espi, 2009). Therefore, although the best signal to use is still up for debate, the palatal click is certainly the most common and preferred signal choice amongst echolocators.

### 1.4.2 Behavioural Investigations of Human Echolocation

Before anything was known about human echolocation, it was theorized that the ability of some blind humans to sense and avoid obstacles in their surroundings was due to ‘facial vision’. It was thought that an object in close proximity would cause slight changes in pressure on the skin, and thus that the face could ‘feel’

the presence of an object. Later, Supa, Cotzin, and Dallenbach (1944) directly tested this notion, and found that blind individuals were unable to detect the presence of an obstacle when their ears were occluded. Therefore, they concluded that the ability of these blind individuals to sense the presence of an obstacle under normal circumstances must be auditory-based. This was later confirmed, and the use of crude echolocation was adopted as an explanation for the participants' obstacle-detecting abilities.

Once it was confirmed that some blind individuals could use echoes to perceive objects, the field of human echolocation enjoyed a brief yet productive period of empirical research. In a classic study on human echolocation, Kellogg (1962) showed that blind individuals could comment on size, distance, and texture based on the echoes that reflected from objects and surfaces. Specifically, Kellogg found that blind participants could detect objects as small as 15 cm in diameter, and also detect the presence of an object at distances ranging from 30 – 120 cm. Furthermore, Kellogg showed that blind participants could discriminate between different materials, such as velvet, glass, and wood.

Rice and colleagues confirmed and expanded on Kellogg's (1962) findings, and showed that blind individuals could comment on the spatial locations of echo-reflecting surfaces with impressive accuracy (Rice, 1967; Rice, 1969; Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965). Following these initial findings, however, research on human echolocation fell out of favour, and it has been only recently that it has regained traction.

The recent work on human echolocation has made significant contributions to our understanding of the technique. For example, using an auditory adaptation of a Vernier acuity task, Teng, Puri, and Whitney (2012) showed that expert echolocators have impressive spatial acuity of approximately 1.2° of azimuth, which is comparable to the thresholds found in bats performing similar tasks and also to acuity in the visual periphery. Furthermore, it has recently been shown that blind echolocators can accurately and reliably extract echo information even from recorded sounds, and can comment on the location, motion, shape, and material properties of objects (Thaler, Arnott, & Goodale,

2011; Thaler, Milne, Arnott, Kish, & Goodale, 2014; Arnott, Thaler, Milne, Kish, & Goodale, 2013). These recent findings have broadened our understanding of human echolocation and have provided numerous avenues for future research.

An important consideration in human echolocation is the fact that under normal circumstances the brain suppresses echoes, a phenomenon called the 'precedence effect' (Wallach, Newman, & Rosenzweig, 1949). This effect describes how when similar sounds occur from different locations with a brief delay, the auditory system suppresses the later sound (i.e. an echo) and gives 'precedence' to the first sound (i.e. the source). This process aids in sound localization because it causes sound reverberations (for example, from walls, ceilings, and other surfaces) to be suppressed and the original source to be attended to. An obvious question, then, is how can people echolocate if their brains suppress echoes? This question was specifically addressed in a recent study with sighted individuals trained on basic echolocation (Wallmeier, Geßele, & Wiegrebe, 2013). The researchers found that the precedence effect still operated, but was significantly reduced during an active echolocation task as compared to a passive listening task. In other words, the precedence effect operated normally (i.e. the echoes were suppressed) only when the echoes were not informative; when the echoes were informative (i.e. in the echolocation task), the precedence effect was reduced and the participants consciously perceived the echoes. Therefore, it is likely that a similar process occurs in blind echolocation experts to support complex echo processing.

### 1.4.3 Neural Correlates of Human Echolocation

In the first neuroimaging study investigating human echolocation, it was found that the calcarine cortices (i.e. what is normally primary visual cortex) of two blind expert echolocators were activated when these individuals perceived objects that were identifiable only by echoes (Thaler et al., 2011). Specifically, their blood oxygenation level dependent (BOLD) activity while listening to binaural recordings of their clicks and the reflected echoes increased not only in auditory, but also in visual cortex. Furthermore, when the investigators isolated the

processing of just the echoes, the BOLD activity was specific to just the visual cortex. Sighted control participants did not show visual cortical activation during the tasks. Therefore, these results suggest that the visual cortex may play a special role in processing echo information in blind expert echolocators.

These initial findings on the neural correlates of echo processing in general set the foundation for investigating how the blind echolocating brain parses and processes specific types of echo features. For example, it has recently been shown that the processing of echoes reflected from a moving surface activated brain areas in the temporal lobe that might potentially overlap 'visual'-motion area MT+, and that this activation showed a contralateral preference in blind echolocation experts (Thaler et al., 2014). In addition, the processing of object shape via echoes activates regions in the ventrolateral occipital cortex, encompassing areas in the lateral occipital complex (LOC), a brain area traditionally involved in visual shape processing (Arnott et al., 2013). Taken together, these findings suggest not only that the processing of echoes may be feature-specific, but also that this processing may make use of what are normally feature-specific visual areas.

## 1.5 The Physical-Acoustic Principles of Echolocation

The following will discuss some of the basic mechanisms thought to operate in the human brain for interpreting the information contained in echoes. The mechanisms discussed below are quite similar to those discussed in the section on bat echolocation because much about human echolocation is inferred from similar processes in bats. Therefore, the discussion of the mechanisms within the context of human echolocation will be brief. To understand these mechanisms, though, we must begin with a basic overview of the human auditory system.

### 1.5.1 The Auditory Pathway

Auditory processing begins at the level of the ear, which is the mechanism for receiving and transducing air perturbations, or sound. The pinna – which is the visible portion of the outer ear made up of folds of cartilage – acts as a receiver

and funnels incoming sounds into the ear canal. The sound then travels to the middle ear which consists of a series of small, delicate bones whose role is to amplify sounds. From the middle ear, sound travels to the inner ear which contains the cochlea. The cochlea is a spiral-shaped, fluid-filled structure that is organized based on frequency, with high-frequency selectivity at the basilar portion and low-frequency selectivity at the apical end. The cochlea is responsive to sounds ranging from approximately 20 – 20,000 Hz, and thus this range of frequencies comprises the human audible range. When a sound enters the cochlea, the frequency components of the sound will perturb the respective frequency sites on the cochlea. The cochlea is also responsive to the intensity of the various frequency components of a sound. These perturbations result in the displacement of hair cells, which then transduce the mechanical perturbation information into an electrical signal which is sent to the brain via the auditory nerve.

After exiting the inner ear, the auditory nerve then projects to brainstem structures, first reaching the cochlear nucleus and then the superior olivary complex. The superior olivary complex is comprised of the lateral superior olive and the medial superior olive, with the former playing a role in the detection of inter-aural level differences (ILD) and the latter a role in inter-aural time differences (ITD). These areas then project to the lateral lemniscus, which then relays the signal to the contralateral inferior colliculus. It is believed that the inferior colliculus plays a role in integrating information from the various brainstem structures, and then projects this information to the medial geniculate nucleus (MGN) of the thalamus. The MGN contains multiple sub-nuclei, each dedicated to a particular function of auditory perception. The MGN is the last subcortical site of auditory processing, with its afferent connections projecting to primary auditory cortex, located along the superior temporal gyrus. The primary auditory cortex is responsible for the processing of basic features of sound, including temporal pattern recognition and pitch change direction. Beyond the primary auditory cortex, sound information is further processed to support aspects of audition such as speech, sound identification, and localization.

The above focused on the ascending connections within the auditory system, but it is also important to discuss the influence of the cortex on the lower-order auditory structures. The cortex projects numerous descending connections that flow down through the structures discussed above in order to modulate their functions. For example, descending connections can help to protect the small bones within the middle ear from high-intensity sounds by causing the surrounding muscles to contract, and can also protect the hair cells in the inner ear by reducing their mobility. Furthermore, the cortex can have a top-down influence on the cochlea by modulating its sensitivity at specific frequencies. This top-down modulation may be particularly relevant in echolocation because the cortex can inform the cochlea to specifically attend to frequencies contained within the signal emission. In addition to modulation at the level of the cochlea, descending connections can also influence activity within the cochlear nucleus to act as a gatekeeper on ascending information. Overall, auditory perception is the product of both ascending and descending connections within the auditory system, and both of these pathways certainly play important roles in perception via echolocation.

### 1.5.2 Using Echoes to Perceive Location

One of the advantages of having two spatially-separated ears is that, depending on where a sound is coming from, the information arriving at the ears will have slight disparities in timing, intensity, and frequency composition. These disparities allow us to determine the azimuthal location of objects with impressive precision, and this is true for source sound localization as well as localization via echolocation. In terms of echolocation, when an individual emits a signal, that signal will come into contact with an object or surface and reflect it back to the listener. Say, for example, that an object is located slightly to the left of centre. The echo that reflects from that object will arrive at the left ear sooner and with a higher intensity than at the right ear. These disparities are termed interaural time differences and interaural level differences, respectively. The reason for these differences is due to the fact that the object in question is closer to the left ear

and also to the fact that the head creates a 'shadow' that attenuates sound. The human auditory system is especially sensitive to these very slight differences, and expert echolocators show remarkable precision in determining the horizontal position of objects via reflected echoes.

### 1.5.3 Using Echoes to Perceive Distance

In the same way that bats can determine distance using FM calls, blind human echolocators can determine the distance of objects because they have the benefit of comparing the time of the emission of their signal to the time of arrival of the echo at the ears. Sound travels at a mostly constant rate (343 m/s at 20°C), so the computations for determining distance need only rely on the signal-echo comparison. An additional advantage for distance computations is that distance information is not confounded or influenced by any other factor (such as size, shape, material, etc.). For example, an object that is close – regardless of any other object properties – will reflect echoes almost immediately. Echoes reflected from an object that is far away, on the other hand, will take longer to arrive at the ears, and thus the individual can conclude that the echo-reflecting surface is far away. Interestingly, humans are quite poor at localizing the distance of source sounds (e.g., a sound emitted from a loudspeaker). For example, while it may be true that loud sounds are typically close and faint sounds are far, the opposite can be true as well. Therefore, echolocation provides a unique advantage for determining the distance of objects due to the ability to compare the timing of signal emission and echo arrival. Because echolocation is not a typical or common method of perception and navigation in humans, it is unclear if – like echolocating bats – human echolocators show neural representations for specific signal-echo delays. It is possible, though, that human echolocators develop new representations or enhance existing ones in order to support distance perception via echoes.

In addition to the information about distance inferred from the timing of signal emission to echo arrival, the distance of echo-reflecting surfaces can also be determined based on repetition pitch. Repetition pitch refers to the



'colouration' of the tone or pitch of a sound as a result of very slight delays (typically less 30 ms) in arrival at the ears between the direct emission and the reflection (Bilsen & Goldstein, 1974; Yost, 1997). In these cases, the listener does not hear an echo *per se*, but rather hears a 'fused' sound that is slightly different in pitch as compared to the emission. This fusion of the direct emission and the reflection also results in an increase in the overall level (i.e. intensity) of the sound at the ears (Schenkman & Nilsson, 2010). Therefore, echo-reflecting surfaces that are located at different distances will differentially affect the overall pitch, and thus this information can be informative for distance discriminations. It is possible that blind echolocators use some combination of absolute timing differences (i.e. delay between the emission and the echo arrival) and repetition pitch, with the overall contribution of either strategy depending on the distance of the surface and other environmental factors.

#### 1.5.4 Using Echoes to Perceive Size

The perception of size via echoes is more complicated than simple location and distance perception, and likely makes use of many of the same mechanisms discussed in the context of bat echolocation. As mentioned earlier, at a basic level, size can be inferred from the overall intensity of the echo: large objects will reflect more of the signal and small objects will reflect less. Furthermore, the echolocator can directly compare the intensity of their emission to the intensity of the echo to infer basic size information. Echo aperture, which represents the angles from which the echoes reflect from the object, can also be useful in determining the size an echo-reflecting surface. It is important to note, however, that both of these cues to object size can be affected by other object properties, such as distance and material. Therefore, the brain must take into account several factors in order to deduce the true object size. This problem is addressed in Chapter 3 of this thesis.

### 1.5.5 Using Echoes to Perceive Shape

The process of inferring shape information from echoes remains comparatively less understood in the context of human echolocation and is specifically addressed in Chapter 2 of this thesis. For two-dimensional objects, it is likely that echolocators trace the edges or contours of the object. In other words, by scanning the object while using mouth clicks (or any echolocation signal), the echolocator can determine the boundaries of the object (i.e. the point at which there is no longer a reflection) and, once the boundary has been determined, can further inspect the edges in order to come to an overall percept of the shape. In terms of three-dimensional shape identification, it is possible that the shape itself can affect the acoustic parameters of the echo. For example, a concave shape will amplify sound relative to a convex shape. In order to identify a three-dimensional shape such as a cube, an echolocator may make use of subtle delay and frequency differences as a result of facets of the cube being closer or farther away. As mentioned above, though, the mechanisms underlying shape identification via echoes remain only crudely understood, and thus further research is necessary.

### 1.5.6 Using Echoes to Perceive Material

Expert echolocators repeatedly report that one of the most salient and informative object cues extracted from echoes are those related to the material properties of objects. This is perhaps not surprising since an echo will necessarily contain characteristics concerning the surface it was reflected from. The fact that echolocation offers the opportunity to compare the emitted signal to the echo has been a common theme in this section. This fact is also of particular relevance to material perception. An echo from a perfect reflector would be identical to the emission in terms of its frequency components. Any deviation away from the frequency components of the emission provides information about the consistency of the reflective surface. As materials become more absorbent, they tend to absorb higher frequencies and reflect lower frequencies. Therefore, if an echolocator emits a click signal (which, as mentioned previously, is typically

broadband) and the echo contains only the lower frequency components, it can be inferred that the reflective surface was made of an absorptive material (i.e., less dense). If almost all of the frequency components of the echo match the click, then the surface was reflective (i.e., more dense). Of course this is a simplification, but echolocators often comment on and discriminate between various types of materials.

## 1.6 Thesis Objectives and General Overview

The overarching goal of the work presented in this thesis was to contribute to our current understanding of human echolocation by examining some of its basic functions, including the perception of the shape, size, and material properties of objects. To address these facets of echolocation, I used both behavioural psychophysical techniques as well as neuroimaging. Given the fact that echolocation can provide for the perception of spatial aspects of the environment similar to vision, and in this way act as a substitute for vision (though with reduced resolution), the experiments within this thesis were planned and discussed with the ‘visual’ nature of echolocation in mind.

The first goal of my thesis work was to determine the role of head movements in the identification of two-dimensional shape, and these findings are presented in Chapter 2. Briefly, I found that blind echolocators were able to accurately identify the shape of two-dimensional objects, but that their ability to do so was dependent on the use of head and body movements to ‘scan’ the objects’ edges. As mentioned above, I addressed my research questions with the ‘visual’ nature of echolocation in mind, and so I suggest that these scanning movements may be similar to the many saccades made by sighted individuals when visually surveying an object or scene.

The second goal of my thesis work was to investigate the possibility that object size perception via echolocation shows size constancy – a perceptual phenomenon associated with vision, and these findings are presented in Chapter 3. The results of the study showed that an expert echocator accurately perceived the true physical size of objects independent of the distance at which

they were located, even though changes to object distance affect size-related echo information. These findings suggest that there may be further parallels between vision and echolocation than previously thought.

My third goal was to determine the neural correlates of material-echo processing, and these findings are presented in Chapter 4. By having expert echolocators listen to recordings of echoes reflected from surfaces of different materials, I show not only that they can determine the material properties of objects, but also that the neural processing underlying this ability may make use of a multimodal visual-auditory-material processing area in the parahippocampal cortex. Again, these results highlight the apparent relationship between echolocation and vision.

Taken together, the work presented in the current thesis makes a significant contribution to our current understanding of human echolocation, and particularly highlights the apparent parallels with vision and visual processing. Overall, the current work supports echolocation as a viable resource for the blind.

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## Chapter 2:

# The Role of Head Movements in the Discrimination of 2D Shape by Blind Echolocation Experts<sup>1</sup>

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## 2.1 Abstract

Similar to certain bats and dolphins, some blind humans can use sound echoes to perceive their silent surroundings. By producing an auditory signal (e.g., a tongue click) and listening to the returning echoes, these individuals can obtain information about their environment, such as the size, distance, and density of objects. Past research has also hinted at the possibility that blind individuals may be able to use echolocation to gather information about 2D surface shape, with definite results pending. Thus, here we investigated people's ability to use echolocation to identify the 2D shape (contour) of objects. We also investigated the role played by head movements, i.e. exploratory movements of the head while echolocating, because anecdotal evidence suggests that head movements might be beneficial for shape identification. To this end we compared the performance of six expert echolocators to that of ten blind non-echolocators and ten blindfolded sighted controls in a shape identification task with and without head movements. We found that expert echolocators could use echoes to determine the shapes of the objects with exceptional accuracy when they were allowed to make head movements, but that their performance dropped to chance level when they had to remain still. Neither blind nor blindfolded sighted controls performed above chance, regardless of head movements. Our results show not only that experts can use echolocation to successfully identify 2D shape, but also that head movements made while echolocating are necessary for correct identification of 2D shape.

## 2.2 Introduction

It is well known that some animals use self-generated sounds to perceive their surroundings via reflected sound waves, or echoes. Echolocation can be used in environments not conducive to vision, thereby allowing animals to navigate and forage even in complete darkness. Similarly, some blind humans have developed the ability to use echoes from self-produced sounds to perceive their silent surroundings. For example, blind echolocators can perceive information such as the size, shape, distance, motion, and material properties of silent objects

(Arnott, Thaler, Milne, Kish, & Goodale, 2013; Kellogg, 1962; Rice, 1967; Rice, 1969; Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965; Schenkman & Nilsson, 2010; Stoffregen & Pittenger, 1995; Teng, Puri, & Whitney, 2012; Teng & Whitney, 2011; Thaler, Arnott, & Goodale, 2011; Thaler, Milne, Arnott, Kish, & Goodale, 2013). In this way, then, echolocation could be considered a crude substitute for vision, allowing blind humans to perceive aspects of their environment that would otherwise go undetected.

Although our knowledge of echolocating animals such as dolphins and some species of bats is quite extensive (for example, see Harley, Putman, & Roitblat, 2003; Schnitzler & Kalko, 2001; Thomas, Moss, & Vater, 2004), comparably little research has been dedicated to understanding the use of echolocation by humans. In the 1940s, it was determined that blind individuals' ability to avoid obstacles and sense the presence of objects was not due to 'facial vision', but to the use of active auditory perception (Ammons, Worchel, & Dallenbach, 1953; Cotzin & Dallenbach, 1950; Supa, Cotzin, and Dallenbach, 1944). Following this discovery, a series of behavioural investigations of echolocation revealed the ability of blind echolocators to detect the presence of objects and also to comment on object features such as size, distance, and material properties (Kellogg, 1962; Rice, 1967; Rice, et al. 1965; Schenkman & Nilsson, 2010; Schörnich, et al. 2013; Teng et al., 2012). Studies have even provided evidence that sighted individuals can learn to echolocate as well (Teng & Whitney, 2011; Ammons et al., 1953).

Although human echolocation is receiving increasing attention in the literature, a clear understanding of the ability of blind echolocators to discern 2D shape is lacking. The perception of shape is likely important to a blind echolocator, for example during navigation where landmark identification and obstacle avoidance are critical. In 1967, Rice reported preliminary results of a 2D shape discrimination task which suggested that blind echolocators could distinguish between a circle, square, and triangle, but he never followed-up on these initial observations. Later, Hausfeld, Power, Gorta, and Harris (1982) showed that untrained sighted individuals could learn to discriminate simple

shapes using echoes, and that a blind participant performed within the range of these sighted individuals. Furthermore, we know from the literature that echolocating bats can perceive the shape of objects from echoes and can use this information to discriminate between food and non-food objects (Simmons & Chen, 1989). Thus, it is reasonable to believe that blind expert echolocators can determine the shape of objects using echoes. What remains unclear in the literature, though, is how the use of movement affects shape identification. We know anecdotally that when expert echolocators are naturally using echolocation they typically make many movements with their head. In fact, almost all of the studies on echolocation from the last century mentioned that their echolocating subjects used head movements that seemed to aid in performance on the tasks, but no research has been done to follow up on these reports. In the context of 2D shape perception, head movements are likely to be useful for resolving the 2D shape of an object, for example by acoustically ‘tracing the contour’ of an object.

In sum, based on the evidence to date, the aim of the current study was two-fold: (1) to determine if blind expert echolocators can use echolocation to identify 2D shapes and (2) to determine if this behaviour is affected by imposing constraints on their head movements. We found that expert echolocators were remarkably accurate at identifying shapes when they were allowed to freely move and explore the objects as they would naturally; when they were required to remain still, however, their performance declined dramatically. The results of the current work contribute to our understanding of the applications of echolocation and show that head movement is crucial to successful object identification (at least in the case of 2D shape perception).

## 2.3 Methods

### 2.3.1 Participants

A total of 26 participants were recruited to participate in a shape identification experiment at The University of Western Ontario (London, Ontario, Canada). All testing procedures were approved by the University ethics board and participants gave written informed consent prior to testing. Participants were drawn from

three different groups: blind expert echolocators (EE) (reported everyday use of active echolocation and extensive experience with the technique), blind controls (BC) (reported little to no use of active echolocation techniques), and blindfolded sighted controls (SC) (reported normal or corrected-to-normal vision and no experience with echolocation techniques). Blind participants who reported any residual vision (for example, bright light detection) were also blindfolded. All participants reported to have normal hearing and no history of hearing difficulties. See Table 2.1 for participant details.

It is important to note that blind and blindfolded sighted controls received no echolocation training prior to participating in the experiment. It is clear from previous research that sighted individuals can learn to use echoes (Teng & Whitney, 2011) and, of course, blind individuals can be trained as well. The purpose of the control participants in the current study, however, was to control for performance that could be attributed to factors other than echolocation expertise (super-sensitivity to echoes as a simple consequence of blindness, ambient sounds, sounds from the movements of the experimenter, etc.). The tongue-click, finger-snap, and other echolocation signals were explained to control participants and they were free to use the technique of their choosing, provided that the ‘signal’ was produced without any external device.

### 2.3.2 Stimuli

Four two-dimensional shapes were presented to all participants: a square (40 cm x 40 cm), a triangle<sup>2</sup> (52 cm x 45 cm [height]), a rectangle oriented horizontally (100 cm x 16 cm), and the same rectangle oriented vertically (see Figure 2.1A). All of the shapes were made of a 0.5-cm thick foam board and covered with

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<sup>2</sup> Please note that the surface area of the triangle is slightly smaller than the other stimuli. This was done to make the triangle ‘visually similar’ in size to the other shapes. We had participants EE1-3 verify that this difference in surface area would not be informative regardless of shape. Furthermore, as also mentioned in the ‘Results’, we confirmed through analysis of error distributions that performance in ‘triangle’ conditions was the same as for the other shapes.

aluminum foil. The shapes were positioned on a 0.6-cm diameter pole, which was determined to be undetectable by echolocation. Before beginning the experiment, all participants were familiarized with the four shapes (sighted controls were allowed only to touch the shapes and not to see them).

### 2.3.3 Procedure

All participants took part in two conditions: A 'free-moving' condition permitting head and body movements, and a 'fixed position' condition not permitting any movement. For both conditions participants EE1, EE2, and EE5 were tested in a Beltone Anechoic Chamber (18 feet high, 23 feet wide, 12 feet deep) at the National Centre for Audiology in London, Ontario, Canada. The chamber is equipped with a 125 Hz cut-off wedge system on the walls and ceiling, and ambient noise recordings indicated a noise floor of 18.6 dB (Larson-Davis System 824). Only participants EE1, EE2, and EE5 were tested in the anechoic chamber due to logistical reasons (i.e. additional participants were not available at the time of testing and the researchers had limited access to the chamber). For free-moving conditions, these participants were also tested in an echo-dampened room (2.75 m x 3 m, four walls covered in 3.8-cm convoluted foam sheets). After determining that there were no performance differences between the anechoic chamber and the echo-dampened room (see Results), we felt it was not necessary to test other participants in the anechoic environment. Therefore, all other participants in all conditions were tested in the echo-dampened room only.

On each trial, one of the four shapes was presented. The presentation height was unique for each participant in order to centre the shapes at ear-level. For the free-moving conditions (Figure 2.1B), participants were situated at a starting position 40 cm away (measured from the ears) and centered on the shape. Once the trial began, participants could freely move their heads and/or bodies to examine the objects via echolocation. For the fixed position condition (Figure 2.1C), participants were situated 80 cm away from the shape and had to

Table 2.1.

*Participant Details for Expert Echolocators (EE), Blind Controls (BC), and Blindfolded Sighted Controls (SC)*

<b>Subject</b>	<b>Sex, Age</b>	<b>Cause of Blindness</b>	<b>Onset</b>	<b>Residual Vision</b>	<b>Echolocation Technique</b>
EE1	M, 45	Retinoblastoma	Early	None	Tongue-click
EE2	M, 29	Glaucoma	Early, progressive	None	Tongue-click
EE3	M, 56	Optic nerve atrophy	Early	None	Tongue-click
EE4	M, 49	Retinoblastoma	Early	None	Speech, tongue-click
EE5	M, 44	Retinopathy of prematurity	Early	None	Tongue-click
EE6	F, 21	Idiopathic intracranial hypertension	Late	Bright light	Finger Snap
BC1	M, 39	Leber congenital amaurosis	Early, progressive	Bright light	Speech, finger snap
BC2	M, 34	Retinopathy of prematurity	Early	Bright light (left eye)	Finger snap, clap
BC3	F, 25	Diabetes	Late	Low level vision (left eye)	Finger snap, clap
BC4	F, 22	Glaucoma, cataracts	Early	Bright light	Speech, clap, finger snap
BC5	M, 44	Retinopathy of prematurity	Early, progressive	Bright light	Speech, finger snap
BC6	M, 20	Leber congenital amaurosis	Early, progressive	Bright light (left eye)	Finger snap
BC7	M, 40	Optic nerve atrophy	Early	None	Clap, finger snap
BC8	F, 60	Retinoblastoma	Early	None	Speech, clap
BC9	F, 24	Retinopathy of prematurity	Early	Bright light	Clap
BC10	F, 32	Optic nerve atrophy	Early	Low level vision	Clap
SC1	M, 30				Clap, speech
SC2	M, 29				Clap, finger snap
SC3	F, 22				Clap
SC4	F, 58				Clap
SC5	F, 31				Clap
SC6	F, 45				Clap, finger snap
SC7	F, 47				Clap
SC8	F, 37				Clap
SC9	F, 35				Clap
SC10	F, 56				Clap, finger snap



keep their head and body still for the duration of the trial. This farther distance (compared to the 40 cm starting distance in the free-moving condition) was reported by three expert echolocators to provide the “best overall impression” of the shape. They mentioned that being any closer to the objects in the fixed position condition would prevent them from gathering object edge information from the echoes. The 80 cm position was used for the fixed position condition, then, to provide the best possible chance for successful performance in these cases. To validate the suggestion given by the expert echolocators, and to rule out distance as a confound, we conducted a control experiment which replicated the ‘fixed head’ conditions, but at a distance of 40 cm (Figure 2.1D). This experiment was conducted only with a subset of participants (EE3, EE6, SC2, SC3).

Throughout the experiment, participants used an echolocation technique of their choice (see Table 2.1) and listened for reflected echoes to determine the shape of the stimulus presented. For the fixed position condition, any participants who chose an echolocation technique other than tongue-clicks or other vocalizations were asked to keep the source of the sound (for example, their hand while finger-snapping) underneath the chin and as close to the body as possible and could not move from that position. For both conditions, participants were given a maximum of 15 seconds per trial and could provide their response at any point within that timeframe (4-alternative forced choice – ‘square’, ‘triangle’, ‘horizontal rectangle’, or ‘vertical rectangle’). For each trial the experimenter measured their response time (i.e. trial start until verbal response onset) using a stopwatch. For each condition, there were a total of 40 pseudo-random trials (10 repetitions per shape, per condition).

## 2.4 Results

For the purpose of the analyses, performance for each participant was collapsed across the four shapes (analyses not shown here revealed no significant differences in the individual shape response patterns for any of the groups). Therefore, the analyses were performed on the overall percentage correct value

for each participant in each of the conditions (free-moving and fixed position). As mentioned in the Methods section, for the free-moving condition participants EE1, EE2, and EE5 were tested in both an anechoic chamber and an echo-dampened room. For each of these participants, we ran t-tests to determine if there were any performance differences between the anechoic chamber and the echo-dampened room. Results for all three participants revealed no significant differences in performance between the two rooms (EE1:  $t(78) = -5.30$ ,  $p = 0.598$ ; EE2:  $t(78) = 1.63$ ,  $p = 0.107$ ; EE5:  $t(78) = -1.113$ ,  $p = 0.269$ ). Therefore, for the purpose of the following analyses we averaged these participants' performance scores across the two testing environments.

A 3 x 2 mixed analysis of variance (ANOVA) was conducted on the data, with between subjects factor 'Group' and within subjects factor 'Condition'. The factor Group included three levels: expert echolocators ( $n = 6$ ), blind controls ( $n = 10$ ), and sighted blindfolded controls ( $n = 10$ ). The factor Condition included two levels: free-moving and fixed position. Because there were fewer participants in the EE group and therefore there could be variability differences across groups, we computed Levene's tests for each condition. The results for both conditions were not significant (free-moving:  $F(2,23) = 2.371$ ,  $p = 0.116$ ; fixed position:  $F(2,23) = 2.61$ ,  $p = 0.095$ ).

The results of the ANOVA revealed a significant interaction between Condition and Group,  $F(2,23) = 38.535$ ,  $p < .0005$ ,  $\eta^2 = .77$  (see Figure 2.2A). Bonferroni-corrected pairwise comparisons revealed that the EE group performed significantly better than both the blind ( $p < .0005$ ) and blindfolded sighted ( $p < .0005$ ) control groups in the free-moving condition. In the fixed position condition, the EE group also performed significantly better than both of the control groups (EE vs. BC:  $p = 0.012$ ; EE vs. SC:  $p = 0.043$ ), but this difference was substantially smaller (EE vs. BC: mean difference = 14.83; EE vs. SC: mean difference = 12.33). The drastic decline in the EE groups' performance in the fixed position condition is easily seen in Figure 2.2A, and pairwise

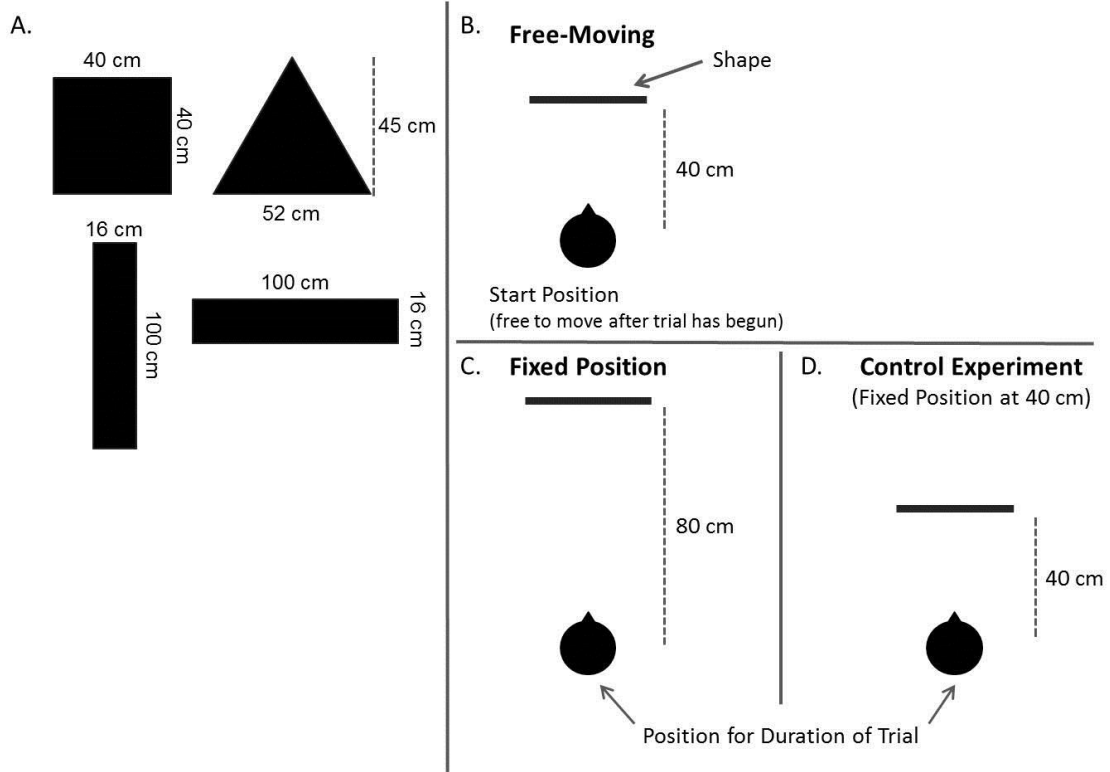


Figure 2.1. Stimuli and procedure for the free-moving and fixed position conditions. Four 2D shapes (A) were presented individually to participants. Shapes were made of foam board and covered in aluminum foil to maximize sound reflection. In the free-moving condition (B), participants were situated 40 cm away from the shape which was centered at ear-level. Once the trial began, participants could move freely in any direction (without touching the shape) in order to identify the shape via echolocation. In the fixed position condition (C), participants were situated 80 cm away from the shape and had to remain in that position for the duration of the trial without making any movements. We also ran a control experiment (D) on a subset of the participants to rule out the possibility of a distance confound between the free-moving and fixed position conditions. For all conditions, participants were given a maximum of 15 seconds per trial to identify the presented shape.

comparisons revealed that the EE group performed significantly better in the free-moving condition ( $p < .0005$ ). The performance of the two control groups in both conditions was statistically indistinguishable (free-moving:  $p = 1$ ; fixed position:  $p = 1$ ). Overall, the results of the interaction show that when the expert echolocators could freely move their heads and bodies they had a substantial advantage and were able to reliably indicate the shape of the object presented to them. When they were required to remain still, however, their ability to indicate the shape of the objects decreased dramatically. Neither of the control groups showed this movement advantage.

To address the possibility that distance differences *per se* were responsible for the decrease in performance in the fixed position as compared to the free-moving condition, we had conducted a control experiment with a subset of participants. This control experiment replicated the fixed position condition, but at the 40 cm position. We used nonparametric related samples McNemar's tests to compare the individual participants' performance on fixed position conditions at each of the two distances. The results of this experiment are shown in Figure 2.2B. The data show that there was no advantage to being located at 40 cm in fixed position conditions. In fact, the EE participants' performance was the same (EE3:  $p = 1$ ) or worse (EE6:  $p = 0.008$ ) than their performance in 80 cm fixed position conditions. The sighted controls showed no significant difference in performance between the two distances (SC2:  $p = 0.5$ ; SC3:  $p = 0.25$ ). In sum, the difference in object distance between free-moving and fixed position conditions could not account for performance differences in the EE group.

Main effects of both Group and Condition were also found ( $F(2,23) = 42.189, p < .0005, \eta^2 = .786$ ;  $F(1,23) = 46.637, p < .0005, \eta^2 = .67$ ). Bonferroni-corrected pairwise comparisons for the main effect of Group revealed that the EE group performed significantly better than both of the control groups (EE vs. BC:  $p < .0005$ ; EE vs. SC:  $p < .0005$ ) but that the control groups performed identically ( $p = 1$ ). Inspection of means showed that the main effect of Condition was due to the fact that, overall, participants performed significantly better in the free-moving condition as compared to the fixed position condition ( $p < .0005$ ). This effect, of

course, was driven by the high performance of the EE group in the free-moving condition, as was shown via the significant interaction.

To supplement the ANOVA analysis, we also ran individual t-tests on each group for each condition comparing performance to chance (25%) and the results were Bonferroni corrected for multiple comparisons. Performance was significantly different from chance only for the EE group in the free-moving condition,  $t(5) = 8.013$ ,  $p < .0005$ . The EE group did not perform significantly better than chance when they were required to remain still ( $t(5) = 2.019$ ,  $p = 0.099$ ) and the BC and SC groups performed at chance level in both the free-moving and fixed position conditions (BC-free:  $t(9) = .023$ ,  $p = 0.982$ , BC-fixed:  $t(9) = -.943$ ,  $p = 0.370$ ; SC-free:  $t(9) = -.103$ ,  $p = 0.920$ , SC-fixed:  $t(9) = .514$ ,  $p = 0.619$ ). The results of the tests against chance are consistent with the ANOVA in that they provide support for a strong advantage for the EE groups in the free-moving condition.

Although the ANOVA allowed us to gain an understanding of the overall performance of the EE group compared to control subjects, it is important to appreciate that, similar to neuropsychological patients, blind echolocators show profound variability in their echolocation abilities as well as their history of use, cause and time of blindness, and so on. Therefore, we felt it was important to also analyze the data by treating each individual echocator as a single case and comparing their performance in both of the conditions to the control participants. To increase statistical power for this analysis, and because the ANOVA revealed no significant differences in performance between the control groups, we combined the control groups for each condition (free-moving and fixed position) for the purpose of this analysis. For each EE participant, we ran modified t-tests to compare their performance to that of the combined control group for both conditions (see Crawford & Garthwaite, 2002; Crawford & Garthwaite, 2007; Crawford & Garthwaite, 2012; Crawford, Garthwaite, & Porter, 2010; Crawford & Howell, 1998). The modified t-test is an extension of the traditional t-test but has been adapted to compare a single case to a control group. For the free-moving condition, the results of the modified t-tests revealed

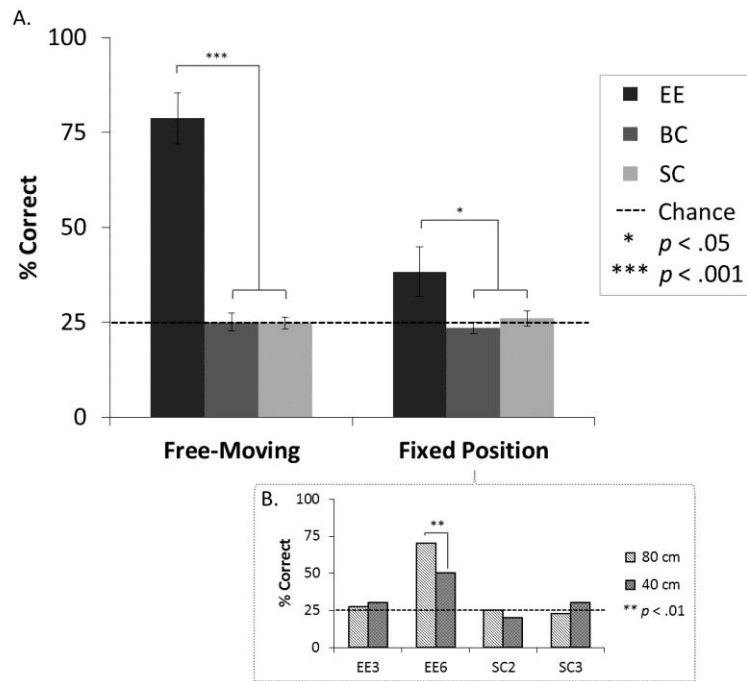


Figure 2.2. Percent correct performance of all groups (expert echolocators [EE], blind control [BC], sighted blindfolded controls [SC]) in each of the two conditions (free-moving and fixed position). Panel A presents the results of the omnibus ANOVA which revealed a significant interaction between the factors (significant differences indicated by asterisks). Error bars represent the standard error of the mean across participants and the dashed line indicates chance performance (25%). Panel B shows the performance of two expert echolocators and two sighted controls who were also tested at the 40 cm position in the fixed position condition. For reference we also show those participants' performance at 80 cm fixed position condition. It is clear from the data that being located closer to the objects in the fixed position condition provided no advantage. In fact, the echolocating participants show comparable (EE3) or worse (EE6) performance at this distance (asterisks indicate a significant difference in performance at the two distances based on results from nonparametric related samples McNemar's tests). These data support our use of the 80 cm position in this condition which, according to the expert echolocators, provided the best overall impression of the shape and thus a better chance of successful performance.

that each individual echolocating participant performed significantly better than the combined control group (see Table 2.2 for all t- and p-values and Figure 2.3A for a graphical depiction of each individual's performance against the control group). The effect size of each echolocator's score also reveals that they reliably performed well above the level of the control group (see Figure 2.3B). In the fixed position condition, however, only participants EE2, EE4, and EE6 performed significantly better than the control group, and the effect size of the difference in performance was substantially lower than in the free-moving condition (with the exception of EE6 who showed high performance in both conditions; see Figure 2.3).

We also ran a 3 (Group) x 2 (Condition) mixed ANOVA on the participants' response times, but this analysis did not reveal any significant results (Condition x Group:  $F(2, 23) = .524$ ,  $p = 0.599$ ,  $\eta^2 = .044$ ; Condition:  $F(1, 23) = 4.14$ ,  $p = 0.054$ ,  $\eta^2 = .153$ ; Group:  $F(2,23) = 2.995$ ,  $p = 0.07$ ,  $\eta^2 = .207$ ). There was a trend toward significance for the main effect of Condition, suggesting that, overall, participants used slightly more time in the free-moving condition, but Bonferroni-corrected pairwise comparisons did not reveal a significant difference.

Overall, the results show that expert echolocators can consistently and reliably indicate the shape of 2D objects when they are allowed to make head and body movements while echolocating. When they are required to remain still, however, performance drops to a level that is statistically indistinguishable from chance. In fact, our single-case analysis shows that in free-moving conditions all our experts perform statistically superior to the control group, whereas only half of them perform superior in fixed conditions. Neither blind nor sighted blindfolded controls showed a movement advantage in the free-moving condition; in fact, their performance was nearly identical in each of the conditions and never deviated from chance.

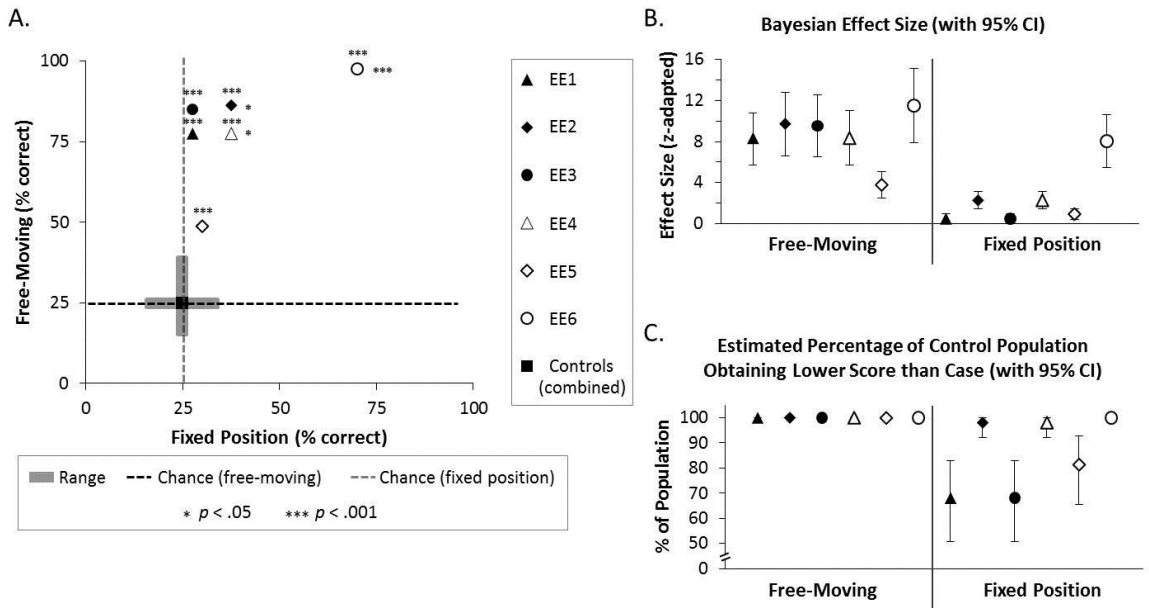
Table 2.2.

*Results of Modified t-test Analysis Comparing Individual Echolocators to Non-echolocating Controls*

Free-Moving							Fixed Position						
Control Sample			Case	Score	Significance Test		Control Sample			Case	Score	Significance Test	
<i>n</i>	Mean	SD			<i>t</i>	<i>p</i>	<i>n</i>	Mean	SD			<i>t</i>	<i>p</i>
20	24.94	6.3	EE1	77.5	8.14	.000	20	24.75	5.61	EE1	27.5	.478	.319
			EE2	86.25	9.495	.000				EE2	37.5	2.217	.019
			EE3	85	9.302	.000				EE3	27.5	.478	.319
			EE4	77.5	8.14	.000				EE4	37.5	2.217	.019
			EE5	48.75	3.687	.000				EE5	30	.913	.186
			EE6	97.5	11.238	.000				EE6	70	7.866	.000

*Note.* Means (control groups only) and case scores are percentage values (percent correct performance). Significance values (*p*) are one-tailed.





*Figure 2.3.* Results of the individual case analyses for the free-moving and fixed position conditions. Each individual echolocator's performance in the free-moving (y-axis) and fixed position (x-axis) conditions are shown in Panel A. The data from the combined control group is also shown, with the shaded bars in each direction indicating the range of scores for each condition. Significant results from the modified  $t$ -tests are indicated by asterisks. Asterisks above a data point indicate a significant difference from the combined control group in the free-moving condition, and asterisks to the right of a data point indicate a significant difference from the combined control group in the fixed position condition (see Table 2.2 for results from all individual tests). Dashed lines in each direction represent chance performance. The Bayesian effect size (with error bars showing 95% confidence intervals (CIs); in some cases CIs are so small that error bars are not visible) for the results of each individual  $t$ -test are shown in Panel B. The effect size was calculated using adapted z scores (Crawford et al., 2010). The 'abnormality' of the case's scores are presented in Panel C which shows the percentage of the control population (with 95% CIs) that would obtain a lower score than the case. The information presented here and in Table 2.2 fully meets the reporting standards set out by Crawford et al. (2010).

## 2.5 Discussion

The aim of the current experiments was to determine if (1) blind expert echolocators can determine the 2D shape of objects by analyzing the echoes reflected from the edges of similar objects, and (2) if movements of the head and body while echolocating are crucial for successful shape identification in our task. The results were clear. Expert echolocators were exceptional at determining the shape of objects that differ only in their edge or contour properties, and they performed well above blind participants who do not echolocate and sighted participants who were blindfolded. When the echolocators were required to remain still, however, performance fell substantially, and was statistically indistinguishable from chance level. Therefore, our results show that blind expert echolocators can use echoes to successfully determine the shape of similar objects, and this ability is critically dependent on the use of head movements. In our study echolocators could move freely, which means that they could perform both angular movements, as well as movements in depth. Future research should aim to investigate the relative contributions of these separate aspects of head motion in more detail.

As mentioned in the Methods, blind and sighted control participants did not receive any explicit echolocation training prior to participation. Not surprisingly then, these participants were unable to successfully use echoes to discern the shape of the objects. This runs contrary to the findings of Hausfeld et al. (1982) who found that untrained sighted participants could identify simple shapes using echoes. Although these participants were untrained, they received feedback on every trial and improvements in performance over the first few trials indicates that this feedback was useful. In fact, the participants in the study reported that during the initial trials they were simply memorizing which echo was associated with which shape, and then applied this knowledge to the remaining trials. It is unclear, then, whether the participants were actually perceiving object shape or were simply relying on subtle differences in echo characteristics without perceiving any shape details. Therefore, the role of feedback, and other

methodological differences, may explain the differences in performance between untrained participants in the current study and in Hausfeld et al.'s experiments.

An important consideration in the design of the experiment is the fact that the distance at which the shape was presented was different for the free-moving and fixed position conditions. Therefore, one could argue that the difference in distance alone may underlie the EE group's decrease in performance in the fixed position condition. We addressed this in our control experiment, and the results of that experiment (see Figure 2.2B) suggest that distance *per se* cannot explain performance differences between free-moving and fixed conditions. Furthermore, if it were the case that distance *per se* could account for performance differences between free-moving and fixed position conditions, we would expect a similar distance effect for all groups, but this was not the case. Finally, we want to highlight once more that the farther position for the fixed position condition was chosen based on echolocators' advice because they found that this distance gave them a better impression of shape as compared to closer distances. This can be understood considering that if an individual is situated very closely to an object and required to remain still, the majority of the echolocation signal will be reflected from the center of the object, thus lacking edge information that could be used to discern the object's shape. One can imagine a similar situation in vision when an individual is situated very closely to an object and is unable to gather information about object features in the periphery without movements of the head and/or eyes. This problem could be solved by simply moving farther away from the object.

A final thing to consider is that more people in the blind control group reported having some residual vision than the expert echolocators (Table 2.1). It is possible that the presence of some residual vision in a blind individual might make them less inclined to develop echolocation as a strategy. But this need not always be the case. Participant EE6, for example, had some residual vision at the time of testing but even so had mastered echolocation and performed better on the task than any of the other expert echolocators. In any case, it seems unlikely that the degree of vision normally available determines how well people

can use echoes to discriminate shape. After all, the blind controls did not perform better than the sighted controls when both groups were blindfolded. Furthermore, the two totally blind individuals (BC7, BC8) in the blind control group performed no better or worse than the rest of that control group, again suggesting that it was expertise *per se* and not degree of blindness that drove performance in our study.

In sum, our results show that blind expert echolocators can use echoes to successfully determine the shape of similar objects, and this ability is critically dependent on the use of head movements.

Head movements made while echolocating may be similar to the multiple eye movements, or saccades, a sighted person makes when visually scanning a large object or a scene. These saccades allow a person to accumulate visual information from the boundaries of a large object and the features of a visual scene, which are then pieced together to create an overall perceptual representation. This process, termed transsaccadic integration, requires the brain to make quick computations of the incoming visual information in order to arrive at a rich and stable representation of an object or scene (Neimeier, Crawford, & Tweed, 2003; Prime, Vesia, & Crawford, 2011). In terms of echolocation in the current study, making head movements while producing tongue-clicks (or other signals) could have provided sound snapshots – or ‘echo saccades’ – that are then automatically pieced together by the brain to provide the individual with a perceptual representation of the object. While transsaccadic integration in vision can occur in a few hundred milliseconds, human echolocation is by comparison much more time-consuming and effortful. Furthermore, the resulting percepts are likely coarser than in vision. In fact, it has been recently shown that the precision of echolocation is comparable to visual acuity in the periphery, which, when compared to foveal acuity, is quite poor (Teng et al., 2012).

Further evidence to support our suggestion that the head movements made by echolocating humans might serve a similar function as visual saccades comes from a recent study on scanning movements in echolocating bats (Seibert, Koblitz, Denzinger, & Schnitzler, 2013). It was suggested that each bat

signal-echo pair was comparable to a visual fixation and that the movements made by the bat between signal-echo pairs are comparable to visual saccades. The researchers found that the bats' scanning behaviours changed depending on the environment they were in and the task they were performing. In particular, when the bats were examining a scene they made large scanning movements but when they detected an object or obstacle the angle of the movements was much smaller. This is quite similar to vision in that the pattern of head and eye movements can be quite different based on if one is looking at a large visual scene – which requires larger, longer movements – or looking at an object within a visual scene – which requires smaller, shorter movements to gain greater object-specific detail (Hardiess, Gillner, & Mallot, 2003; Rayner, 1998). Considering these findings in echolocating bats and our results showing the advantage of using head movements in human echolocation, it is important for future research to address the different types of movements made by expert echolocators and how these movements change in different environments and tasks.

Although it is quite clear that head movements – or 'echo saccades' – seem to facilitate 2D shape perception in echolocation, one of our echolocating participants, EE6, showed impressive performance in both of the conditions. An important consideration is the fact that EE6 used a finger-snap as opposed to the tongue-click signal used by the other echolocating participants. As mentioned in the Methods section, any participants who used a signal other than tongue-clicks or other vocalizations had to keep the source of the signal (in this case, the hand) close to the body, under the chin, and as still as possible. It is possible, however, that slight movements were made that were not noticed by the researcher and possibly not even by the participant herself, and that these might have aided performance. One might also consider the choice of signal *per se* aiding performance, i.e. EE6 used a finger snap whereas the other EEs used tongue clicks. Yet, several of the control participants used finger snaps as well, without the advantage we saw in EE6.

In addition to being potentially relevant for explaining EE6's impressive performance, the question of the choice of signal is also relevant for the current study because the majority of control participants used a signal that was different from the echolocating participants (with the exception of EE6). It is important to note, though, that even though the majority of our EE participants used tongue-clicks, this is not to say that they use this type of signal exclusively in everyday life. In fact, almost all of the echolocators report using claps, finger-snaps, and other techniques. So, the variety of signals used by echolocators in real life – and the various signals used by participants in the current study – raises an important question: what is the best signal to use for echolocation? This question has been addressed previously (Rojas, Hermosilla, Montero, & Espi, 2009; 2010) but a consensus is lacking. For example, longer signals (500 ms) may be better than shorter ones because they result in a surplus of echo information due to repetition pitch (Schenkman & Nilsson, 2010). Also, it has been suggested that noise signals provide more and better information than click signals (Arias & Ramos, 1997), though it has also been suggested that in particular the palatal tongue click is the best signal for echolocation (Rojas et al., 2009). Therefore, it is unclear whether participants' choice of signal in the current study could have directly affected performance (regardless of movement) because there is no clear indication of what is the best echolocation signal. Also, it is important to note that most systematic studies of the signals used in echolocation (and many studies on echolocation in general) use artificial sounds played by a loudspeaker or through headphones. Therefore, it is important for future research to address the use of self-produced signals in order to better understand the use of natural, active echolocation and maximize the information content of echoes.

It can be argued that, at a basic level, the ability to echolocate involves some combination of increased echo sensitivity (Dufour, Després, & Candas, 2005; Kolarik, Cirstea, & Pardhan, 2013), suppression of the precedence effect (Wallmeier, Gebele, & Wiegrebe, 2013), and, of course, intact hearing (Schenkman & Nilsson, 2010). This is encouraging because it means that the ability to echolocate is available to all people, blind or sighted. Therefore, we

believe that the use of echolocation should be more actively promoted in the blind community because, even if one learns to echolocate only at a very basic level, it would provide another resource for perceiving one's surroundings and gaining further independence in life. In fact, a recent survey has shown that the use of echolocation by the blind may have real-world advantages (Thaler, 2013). In particular, blind echolocators have higher salaries and greater mobility in unfamiliar places than blind individuals who do not echolocate. Of course, other variables likely mediate these advantages, but even the additional information that an echocator possesses about his surroundings – which then aid in obstacle avoidance, navigation, and object perception – is an advantage in itself.

Overall, the results of the current experiments show that active echolocation is a useful resource that allows blind individuals to gather accurate object shape information from faint echoes. Even this basic application of echolocation shows how useful it can be, by providing blind individuals with perceptual information that they would otherwise not have access to. Considering echolocation is a trainable skill, there is great potential to offer valuable and liberating opportunities for the blind and visually-impaired.

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## Chapter 3:

### A Blind Human Expert Echolocator Shows Size Constancy for Objects Perceived by Echoes<sup>3</sup>

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Milne, J.L., Anello, M., Goodale, M.A., & Thaler, L. A blind human expert echolocators shows size constancy for objects perceived by echoes. *Neurocase*, doi:10.1080/13554794.2014.922994.

### 3.1 Abstract

Some blind humans make clicking noises with their mouth and use the reflected echoes to perceive objects and surfaces. This technique can operate as a crude substitute for vision, allowing human echolocators to perceive silent, distal objects. Here we tested if echolocation would, like vision, show size constancy. To investigate this, we asked a blind expert echolocator to echolocate objects of different physical sizes presented at different distances. The expert echolocator consistently identified the true physical size of the objects independent of distance. In contrast, blind and blindfolded sighted controls did not show size constancy, even when encouraged to use mouth-clicks, claps, or other signals. These findings suggest that size constancy is not a purely visual phenomenon, but that it can operate via an auditory-based substitute for vision, such as human echolocation.

### 3.2 Introduction

A number of studies have confirmed the ability of blind human echolocators to extract information from echoes about object features such as shape, location, motion, and material (for reviews see Stoffregen & Pittenger, 1995; Kolarik, Cirstea, Pardhan, & Moore, 2014). Furthermore, echoes are informative for determining the size and distance of objects (Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965; Teng & Whitney, 2011). Although it has been confirmed that expert echolocators can extract size and distance information from echoes in isolation, there has been no direct investigation on the echolocation of these factors in combination.

Integrating size and distance cues is critical for accurate perception of object size. For example, the visual system must overcome the fact that altering the distance of an object from the eyes results in changes to the size of the retinal image. Despite the differences in retinal image size, however, people's percept reflects the true physical size of the object. This perceptual phenomenon has been termed size constancy (Holway & Boring, 1941).

In echolocation a similar situation may arise. Specifically, the size of the acoustic angle of a sound-reflecting surface decreases as its distance increases. Importantly, changes in the size of a sound-reflecting surface (regardless of changes in distance) lead to changes in both the level and spectrum of the reflected sound (e.g., Heinrich, Warmbold, Hoffmann, Firzlaff, & Wiegrebe, 2011). At the same time, the distance of a sound-reflecting surface is reliably coded via pulse-echo delays. Hence, the acoustic information present in echolocation is sufficient for accurate computation of the physical size of a sound-reflecting surface. Given that the human brain shows size constancy in at least one modality (i.e. vision), and given that echolocation in principle provides the information necessary to achieve size constancy, we were interested if size constancy is also supported for objects perceived via reflected echoes.

To test this, we recruited a blind human expert echolocator (EE) who lost his sight in early infancy due to idiopathic optic nerve atrophy and has no residual vision. EE developed echolocation techniques on his own during early childhood and attributes his first realizations of the possible utility of echoes to hearing the sound of his father hitting a metal fence post with a hammer. He noticed that the hammering sound reflected from the walls and other surfaces around him, and realized that these echoes provided a rich source of information, particularly for obstacle avoidance. As time went on, he learned that he could produce his own sounds, such as mouth-clicks. Now in his late fifties, EE continues to use echolocation on a daily basis.

### 3.3 Methods

#### 3.3.1 Participants

As mentioned above, we recruited one blind expert echolocating participant (male, 57 years old at time of testing). Hearing tests revealed that EE's pure tone thresholds were within the range of a young normative sample up to 4 kHz and that he showed mild hearing loss beyond 4 kHz, consistent with his age. As control groups, we recruited 10 blind participants (five female; mean age = 35.9) and 10 blindfolded sighted participants (five female; mean age = 40.4). All control

participants reported normal hearing and no prior experience with echolocation. Sighted participants reported no history of visual disorders. All participants were blindfolded (including EE and blind control participants) and took part in three experiments (detailed below) at The University of Western Ontario (London, Ontario, Canada). The experiments took place in an echo-dampened room (2.75 m x 3 m, four walls covered in 3.8-cm convoluted foam sheets, carpeted floor). All testing procedures were approved by the University ethics board and participants gave written informed consent prior to testing.

### 3.3.2 Stimuli and General Procedure

Objects used in the experiments included three physical sizes of circles and horizontally-oriented rectangles (Figure 3.1A). The shapes were designed so that the medium-sized shape was twice the size of the small shape, and the large-sized shape was three-times the size of the small shape. Furthermore, each size of circle and rectangle were near-equated in total area. In accordance with the proportional size relationship between the objects, the distances were chosen so that the middle location was twice the distance of the near location, and the far location was three times the distance of the near location. Although shape is not a relevant cue for size constancy, we included the different shapes to increase the attentional demands of the tasks. The objects were positioned on a 0.6-cm diameter pole and could be placed at one of three distances (Figure 3.1B). The objects and distances used depended on the particular experiment being run, and each one of the experiments is detailed below. Before beginning the experiments, all participants were familiarized with the objects (sighted controls were allowed only to touch the objects and not to see them).

Before the beginning of each trial, one object was positioned directly ahead of the participant and centered on the ears (i.e. presentation height was unique for each participant). During this object-placement period between trials, participants wore ear-bud headphones playing white noise to mask any noise cues related to changing the stimulus display. Once the trial began, participants were given a maximum of 20 seconds to scan the object using the echolocation

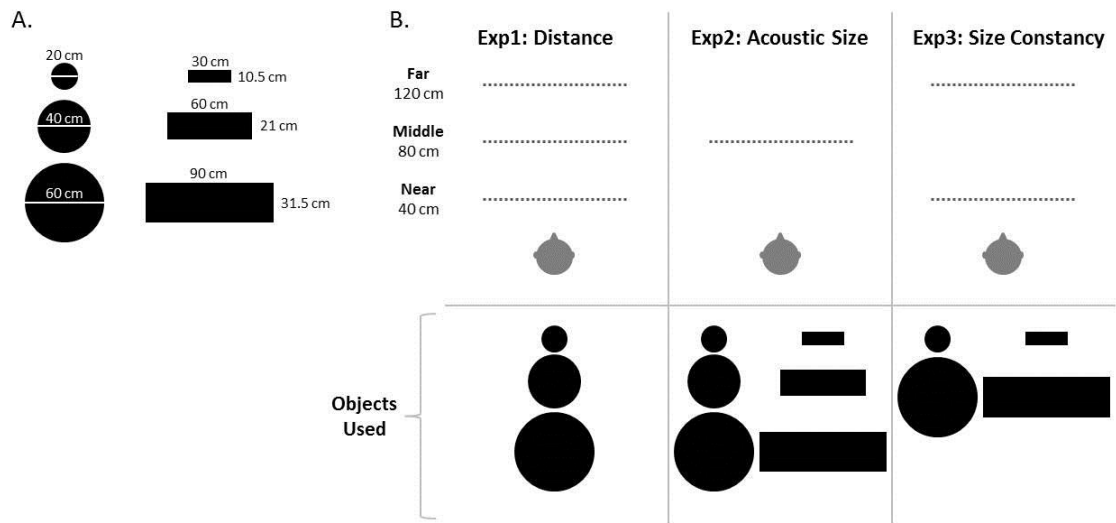


Figure 3.1. Stimuli and procedure for Distance, Acoustic Size, and Size Constancy experiments. A) The possible objects to be used in each of the experiments included three physical sizes of circles and rectangles (the medium-sized objects were double the size of the smallest objects, and the large objects were triple the size of the smallest objects). The objects were created from 0.5-cm thick foam board and covered with aluminum foil and were positioned on a 0.6-cm diameter pole. B) The basic layout is shown for each individual experiment. The top panel shows the distance(s) at which the objects could be placed (specific objects used in each experiment are shown in the bottom panel). Note that the spacing of the distances is proportional to the sizes of the objects (i.e. the middle position is twice the distance of the near position, and the far position is three times the distance of the near position). For all tasks, participants stood and were permitted to move side-to-side as well as up and down to allow them to scan the object (for a maximum of 20 seconds) but were not permitted to move toward or away from the object. Note that for Experiment 3 only the near and far positions and small and large objects were used. This allowed for a direct test of size constancy.

technique of their choice. Participants stood for the duration of all experiments and were allowed to make slight movements from side-to-side and up and down, but not toward or away from the object. Participants provided verbal responses for each experiment.

It is important to note that blind and blindfolded sighted controls received no echolocation training prior to participating in the experiment. The reason for this was that the purpose of the control participants in the current study was to control for performance that could be attributed to factors other than echolocation expertise (for example, neuroplasticity due to blindness, ambient sounds, sounds from the movements of the experimenter, etc.). The mouth-click, finger snaps, and other echolocation signals were explained to control participants and they were free to use the technique of their choosing.

### 3.3.3 Experiment 1: Distance

To investigate the ability to detect distance information, we used three circular objects and presented them in isolation at any of the three distances (Figure 3.1B). The participants' task was to determine only the distance of the object, for which they provided a verbal response ("near", "middle", "far"). There were a total of 36 trials, with four repetitions of each object size at each distance.

### 3.3.4 Experiment 2: Acoustic Size

To investigate the detection of size, we utilized six objects (three circles and three rectangles) but presented them only at the middle distance. The participants' task was to determine both the size and shape of the object (e.g., "small circle", "medium rectangle"). Since distance was kept constant in Experiment 2, identification of size in these cases was equivalent to identification of acoustic size (i.e. area in degrees of acoustic angle), but it did not require size constancy. There were a total of 36 trials, with six repetitions of each object.

### 3.3.5 Experiment 3: Size Constancy

To examine size constancy, i.e. correct perception of physical size, we designed the experiment in accordance with the principles of visual size constancy. That is,



we used only the small and large objects (circles and rectangles) and placed them only at the near and far distances. The small objects at the near location would have the same acoustic size (i.e. same echo intensity and aperture) as the large objects at the far position. The participants' task was to indicate the size and shape of the object (e.g., "small rectangle", "large circle"). There were a total of 40 trials, with five repetitions of each object at each location.

## 3.4 Results

### 3.4.1 General Details

Our initial analyses were aimed at determining if there were any differences in performance between the blind and sighted control groups for each of the three experiments. To do this, we ran mixed analysis of variance (ANOVA) tests, with the experimental manipulations as the repeated variable, and 'group' as the between subjects variable for each experiment. The analyses revealed no significant effect of 'group' for any of the three experiments (Figure 3.2).

Therefore, for all subsequent analyses we combined blind and sighted control groups into a single control group.

To compare EE's performance to controls, we ran two types of analyses. First, we used t-tests and effect size measures modified to compare a single case to a control group (Crawford, Garthwaite, & Porter, 2010; Crawford & Howell, 1998). The analyses were conducted on the overall percentage correct performance of EE and the combined control group in each experiment. We supplemented these analyses by comparing both EE's and the combined control group's performance to chance for each experiment using binomial tests and traditional t-tests, respectively. Instead of overall performance, we performed these analyses on the separate conditions within each experiment. An initial analysis had revealed no differences between circular and rectangular shapes for Experiments 2 and 3. Thus, for subsequent analyses, performance was collapsed across shape.

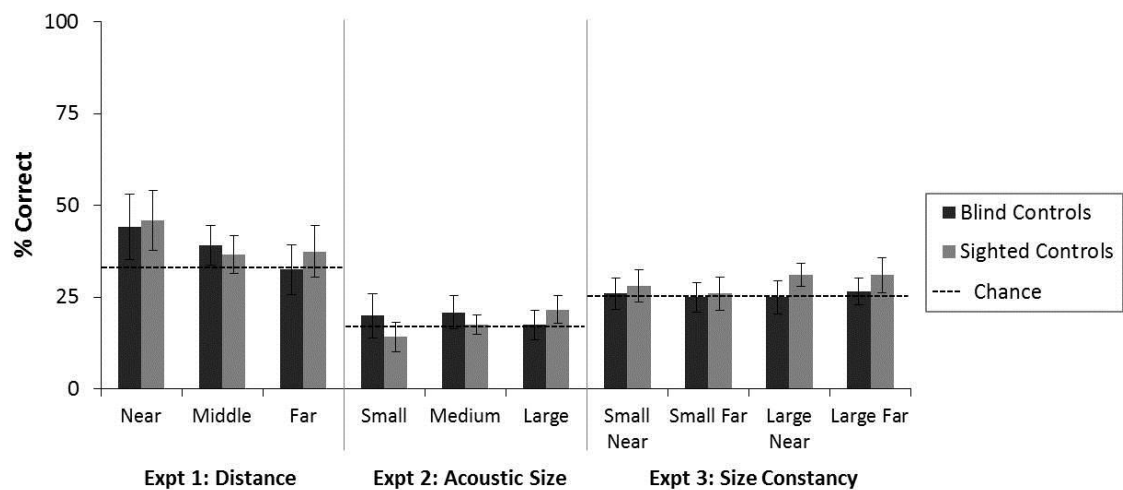


Figure 3.2. Average percent correct performance (+/- SEM) of the blind non-echolocating and blindfolded sighted control groups on the Distance, Acoustic Size, and Size Constancy experiments. Mixed analysis of variance tests for each of the three experiments revealed no significant main effects or interactions for any of the three experiments (similarities in performance are easily seen in the figure). Therefore, for all subsequent analyses the control groups were combined to form a single control group.

### 3.4.2 Experiment 1: Distance

The modified t-test revealed that EE performed significantly better than the combined control group on the distance discrimination task (see Figure 3.3A and Table 3.1). Comparisons to chance revealed that EE performed well above chance level (33%) at each of the distances (near:  $p = 0.004$ ; middle:  $p = 0.004$ ; far:  $p = 0.018$ ), while the control group's performance was statistically indistinguishable from chance at each distance (near:  $t(19) = 2.043$ ,  $p = 0.055$ ; middle:  $t(19) = 1.347$ ,  $p = 0.194$ ; far:  $t(19) = 0.418$ ,  $p = 0.681$ ) (see Figure 3.4A).

### 3.4.3 Experiment 2: Acoustic Size

As mentioned above, the responses from Experiment 2 were collapsed across shape. The modified t-test analysis revealed that EE performed significantly better than the combined control group (see Figure 3.3A and Table 3.1). Additional analyses comparing performance to chance revealed that EE performed well above chance level (16.67%) for each of the different sizes (small:  $p = 0.008$ ; medium:  $p < 0.001$ ; large:  $p < 0.001$ ) (see Figure 3.4A). Again, the combined control group's performance did not differ from chance for any of the object sizes (small:  $t(19) = 0.117$ ,  $p = 0.908$ ; medium:  $t(19) = 0.972$ ,  $p = 0.343$ ; large:  $t(19) = 1.071$ ,  $p = 0.297$ ).

### 3.4.4 Experiment 3: Size Constancy

As mentioned above, Experiment 3 was aimed at determining if an expert echolocator can integrate acoustic size and distance information to determine the true physical size of objects. Again, the responses for this experiment were collapsed across shape. The modified t-test analysis revealed that EE performed well above the level of the combined control group (see Figure 3.3A and Table 3.1). In fact, EE's best performance across all three experiments was in Experiment 3. Comparisons against chance revealed that EE performed significantly better than chance level (25%) in three of the conditions (small-near:  $p < 0.001$ ; large-near:  $p < 0.001$ ; large-far:  $p < 0.001$ ) but his performance failed to reach significance for the small object at the far position ( $p = 0.078$ ). It is important to note, though, that EE's performance in this condition was largely

driven by errors in shape and not in size (see Figure 3.4B). The combined control group did not show above chance performance for any of the conditions (small-near:  $t(19) = 0.667$ ,  $p = 0.513$ ; small-far:  $t(19) = 0.17$ ,  $p = 0.867$ ; large-near:  $t(19) = 1.082$ ,  $p = 0.293$ ; large-far:  $t(19) = 1.255$ ,  $p = 0.225$ ).

Overall, the results of Experiments 1 and 2 confirm the ability of a blind expert echolocator to determine the distance and acoustic size of objects independently. This agrees with previous reports in the literature (Rice & Feinstein, 1965; Rice et al., 1965). Most importantly, however, Experiment 3 goes beyond this and shows that a blind expert echolocator can determine the true physical size of an object independent of its distance. Therefore, these results suggest that size constancy operates for object size perception via echolocation.

### 3.5 Discussion

The aim of the current experiment was to determine if size constancy – a perceptual phenomenon linked to vision – also operates for echolocation. We showed for the first time that a blind human expert echolocator could consistently and reliably indicate the true physical size of objects independent of the distance at which they were located. Blind non-echolocators and blindfolded sighted controls did not show size constancy, suggesting that echolocation expertise rather than neuroplasticity due to blindness or ambient sounds was responsible for EE's performance.

These findings support the use of echolocation as a viable and useful resource for the blind, because the ability to accurately determine the physical size of objects has immediate benefits for navigation in the physical world. In addition, the current findings broaden our basic understanding of the technique. For example, previous studies using functional magnetic resonance imaging have implicated 'visual' brain areas for echolocation (Arnott, Thaler, Milne, Kish, & Goodale, 2013; Thaler, Arnott, & Goodale, 2011; Thaler, Milne, Arnott, Kish, & Goodale, 2014). The current findings suggest further parallels between vision and echolocation, in that both modalities show size constancy. This suggests that

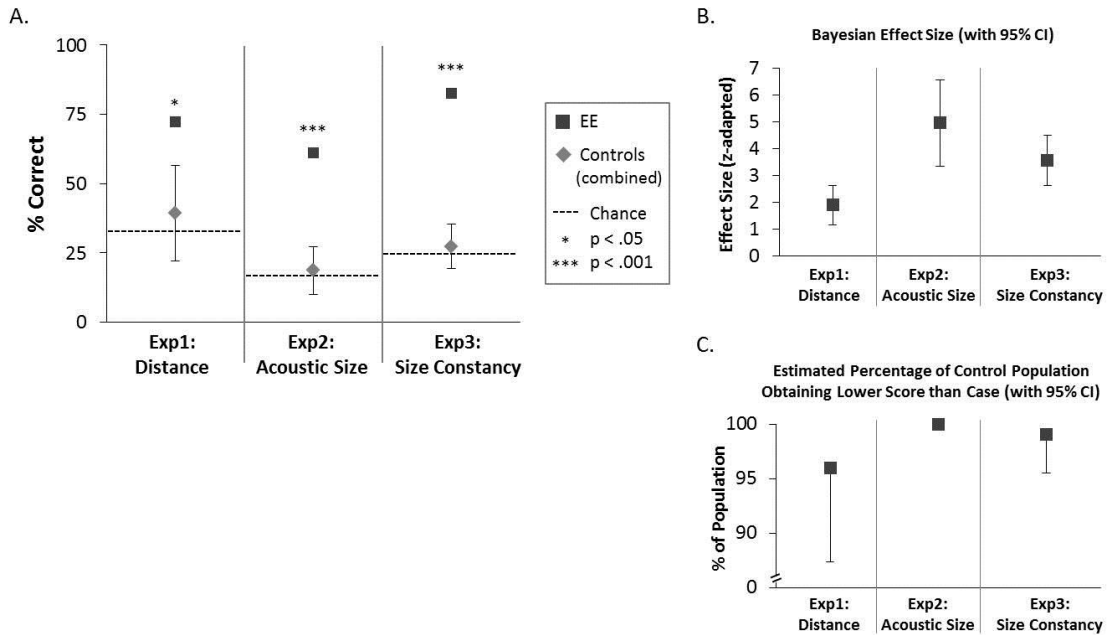


Figure 3.3. Results of the individual case analyses for the Distance, Acoustic Size, and Size Constancy experiments. Panel A shows the results of the modified t-tests comparing the expert echolocator's overall performance (as percent correct) to the combined control group's performance. Significant differences are indicated by asterisks. The Bayesian effect sizes (with error bars showing 95% confidence intervals (CIs)) of each individual t-test are shown in Panel B. The effect size was calculated using adapted z scores (Crawford et al., 2010). The 'abnormality' of the case's scores are presented in Panel C which shows the percentage of the control population (with 95% CIs) that would obtain a lower score than the case.

Table 3.1.

*Results of the modified t-test analysis comparing EE's overall performance to the overall performance of the combined control group in each of the three experiments.*

Experiment	EE's Score	Control Sample			Significance	
		n	Mean	SD	t	p
1. Distance	72.22	20	39.31	17.37	1.85	0.039
2. Acoustic Size	61.11	20	18.61	8.55	3.671	< 0.001
3. Size Constancy	82.5	20	27.31	8.11	6.638	< 0.001

Note: The modified t-test is a version of the classic t-test used to compare the performance of a single case against a control group. Means (control group only) and case scores are percentage values (percent correct performance). Significance values (p) are one-tailed.

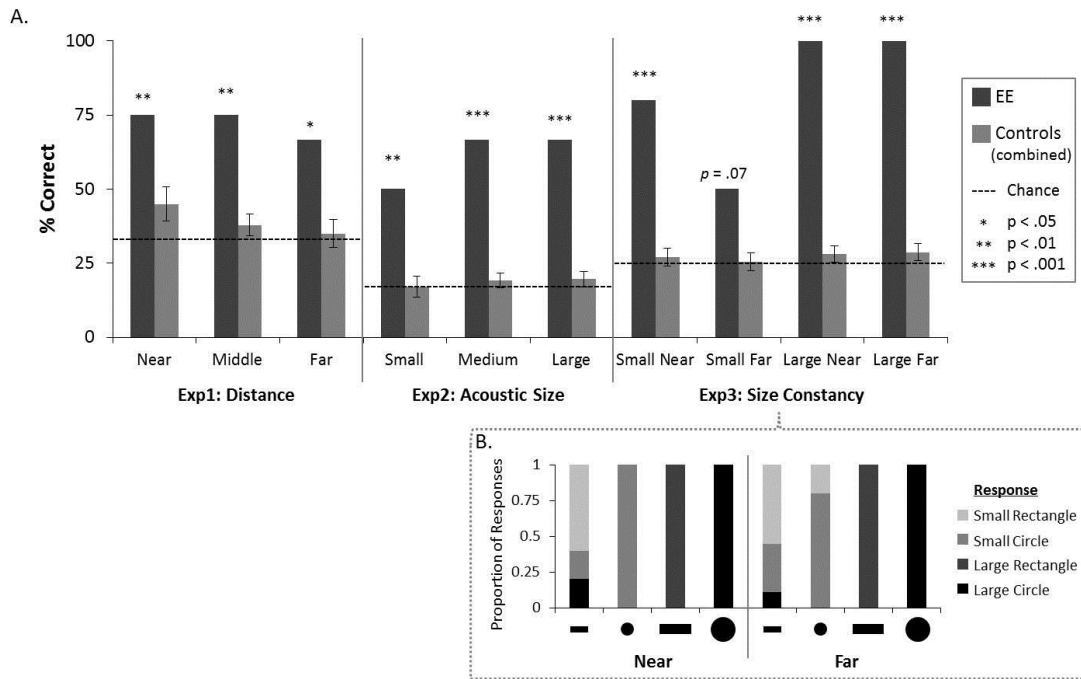


Figure 3.4. Results from tests against chance for the expert echolocator (binomial tests) and combined control group (t-tests). Participants' performance (shown as percent correct) was collapsed across shape for Experiments 2 and 3. Chance performance for each of the tasks is indicated by the dashed lines and significant results are indicated by asterisks. The distribution of EE's responses (B) is shown for the size constancy task. Although EE performed statistically at chance for the 'small-far' condition, the error distributions show that this decrease in performance was driven by errors in shape judgement and not size judgement, thus supporting size constancy in these cases.

similarities in brain activity may also signify similarities in terms of behavioral principles, and future research should address these possibilities.

As laid out in the introduction, at a general level, object size information can be inferred from the overall intensity of the echo as well as spectral changes caused by the 'spread' of angles from which the echoes arrive at the ears (aperture). The contribution of each of the cues may depend on the size of the object, with evidence suggesting that overall intensity cues are best suited for smaller objects whereas aperture cues are most relevant for larger object widths, at least in the case of echolocating bats (Heinrich et al., 2011). Furthermore, there are binaural cues to size (Holderied & von Helversen, 2006). In terms of object distance, the cue that indicates distance most reliably is the time delay between the outgoing signal and the returning echo, and this cue is independent from other aspects of the sound. Thus, echolocation has information sufficient for size constancy.

Although the current study is the first investigation of size constancy in human echolocation, Heinrich and Wiegrebe (2013) tackled the question in the context of bat echolocation. Interestingly, based on their results the researchers suggested that bats do not show size constancy, at least for the perception of virtual objects. This is curious, because echolocating bats do encode both object aperture (i.e. acoustic size) (Heinrich et al., 2011) and pulse-echo delays (i.e. distance) (Wenstrup & Portfors, 2011). Therefore, it is surprising that bats would not show size constancy considering the clear neural representation of both size and distance. Contrary to these unresolved findings in bats, our results clearly show that a human echolocator has stable, absolute size perception. Considering that human echolocators may lack the sophisticated neural mechanisms that have evolved in bats, our findings, then, warrant further investigation into potential size constancy mechanisms in bats and other echolocating species.



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Chapter 4:  
Parahippocampal Cortex is involved in Material Processing  
via Echoes in Blind Echolocation Experts<sup>4</sup>

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<sup>4</sup> A version of this chapter has been accepted pending revisions:

Milne, J.L., Arnott, S.R., Kish, D., Goodale, M.A., & Thaler, L. Parahippocampal cortex is involved in material processing via echoes in blind echolocation experts. *Vision Research*, accepted pending revisions.

## 4.1 Abstract

Some blind humans use sound to navigate by emitting mouth-clicks and listening to the echoes that reflect from silent objects and surfaces in their surroundings. These echoes contain information about the size, shape, location, and material properties of objects. Here we present results from an fMRI experiment that investigated the neural activity underlying the processing of materials through echolocation. Three blind echolocation experts (as well as three blind and three sighted non-echolocating control participants) took part in the experiment. First, we made binaural sound recordings in the ears of each echolocator while he produced clicks in the presence of one of three different materials (fleece, synthetic foliage, or whiteboard), or while he made clicks in an empty room. During fMRI scanning these recordings were played back to participants. Remarkably, all participants were able to identify each of the three materials reliably, as well as the empty room. Furthermore, a whole brain analysis, in which we isolated the processing of just the reflected echoes, revealed a material-related increase in BOLD activation in a region of left parahippocampal cortex in the echolocating participants, but not in the blind or sighted control participants. Our results, in combination with previous findings about brain areas involved in material processing, are consistent with the idea that material processing by means of echolocation relies on a multi-modal material processing area in parahippocampal cortex.

## 4.2 Introduction

Like animals such as bats and dolphins, a subset of blind humans can use echoes from self-produced signals to localize and identify silent objects and surfaces in their environment. For example, by interpreting the echoes of their mouth-clicks, these individuals can report on features such as the size, shape, location, distance, motion, and material (or texture) of objects (Arnott, Thaler, Milne, Kish, & Goodale, 2013; Hausfeld et al, 1982; Kellogg, 1962; Rice, 1967; Rice, 1969; Rice & Feinstein, 1965; Rice, Feinstein, & Schusterman, 1965; Schenkman & Nilsson, 2010; Stoffregen & Pittenger, 1995; Teng, Puri, &

Whitney, 2011; Teng & Whitney, 2011; Thaler, Arnott, & Goodale, 2011; Thaler, Milne, Arnott, Kish, & Goodale, 2013; for review, see Kolarik, Cirstea, Pardhan, & Moore, 2014). Because echolocation allows blind individuals to perceive silent objects from a distance, it can be thought of as an alternative to vision; without the use of echolocation the perception of such objects would be impossible with the remaining senses.

In the first functional magnetic resonance imaging (fMRI) investigation on human echolocation, it was found that the calcarine cortices (i.e. BA17, what is typically referred to as primary visual cortex in sighted people) of two blind expert echolocators were activated when these individuals perceived objects that were identifiable only by echoes (Thaler et al., 2011). Specifically, their blood oxygenation level dependent (BOLD) activity while listening to binaural recordings of their clicks and the reflected echoes increased in not only auditory, but also calcarine cortex. Even more, when they isolated the processing of just the echoes, the BOLD activity was specific to just the calcarine cortex. Sighted control participants did not show calcarine cortical activation during the tasks.

These initial findings on the neural correlates of echo processing in general set the foundation for investigating how the blind echolocating brain parses and processes specific types of echo features. For example, we have recently shown that the processing of echoes reflected from a moving surface activated a brain area in temporal-occipital cortex that potentially corresponds to 'visual'-motion area MT+, and that this activation showed a contralateral preference (Thaler et al., 2014). In addition, we have shown that the processing of object shape via echoes activates areas in the ventrolateral occipital cortex, encompassing areas in the lateral occipital complex (LOC), a brain area traditionally involved in visual shape processing (Arnott et al., 2013). Taken together, these findings suggest not only that the processing of echoes may be feature-specific, but also that this processing may make use of what are normally feature-specific visual areas.

Several of the expert echolocators whom we have studied have anecdotally remarked on the saliency and utility of information about material that

they routinely get from echoes, particularly in terms of navigation, orientation, and obstacle avoidance. For example, the stark difference in material (and thus the reflected echoes) between a concrete sidewalk and adjacent grass provides useful information for discerning the path ahead while walking or bike-riding. Previous behavioural investigations have shown that people can use echolocation to discriminate between reflective materials such as metal and glass and more absorptive materials such as velvet and denim (Hausfeld et al., 1982; Kellogg, 1962).

The neural basis underlying this skill is poorly understood, however. With respect to visual perception of material properties, fMRI research suggests the involvement of collateral sulcus (CoS) and the parahippocampal cortex (PHC) (Cant & Goodale, 2007, 2011; Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010; Hiramatsu, Goda, & Komatsu, 2011; Jacobs, Baumgartner, & Gegenfurtner, 2014). With respect to the auditory modality, previous research suggests the involvement of right parahippocampal cortex (Arnott et al., 2008). Importantly, areas in right PHC responding to auditory materials also responded to visual surface materials, thus suggesting the existence of a visuo-auditory multimodal material processing area in PHC. Auditory materials in the context of Arnott et al. (2008) were conveyed through sounds of materials being manipulated, i.e. materials were manipulated with the hands to produce a material conveying sound, such as crumpling of paper. During echolocation, in contrast, the material is conveyed through the reverberation of a vocalization off the material, whilst the material itself remains distal and silent. Thus, one may expect a difference in terms of how the brain processes material conveyed through echoes. Accordingly, we conducted a previous study into echolocation of material, alongside echolocation of shape (Arnott et al., 2013), but the results of this study with respect to brain activation specific to material echoes were inconclusive. This could potentially be due to the design of the task in which echo-acoustic information conveying shape was not acoustically independent from echo-acoustic information conveying material properties, rendering a comparison of material echoes regardless of shape essentially impossible.

Consequently, the current study addressed the perception of material echoes per se; that is, in the absence of any other object or spatial cues. Three blind expert echolocators, three blind, and three sighted control participants took part in the experiment. Our results revealed a material-echo related increase of activation within left parahippocampal cortex in all three expert echolocators. This activation was absent in sighted and blind control participants. We did not find material echo related activations in posterior CoS, suggesting that some of the brain areas previously implicated for visual processing of materials were not involved. Our results further support the idea of feature-specific echo processing and also contribute to the possibility of a multimodal material processing area within parahippocampal cortex.

### 4.3 Materials and Methods

All testing procedures were approved by the ethics board at the University of Western Ontario, and participants gave written, informed consent prior to testing. All experimental procedures conformed to The Code of Ethics of the World Medical Association as stated in the Declaration of Helsinki (1964). The consent form was read to participants, and the location to sign was indicated through tactile and visual markers.

Software used to conduct testing was programmed using Psychophysics Toolbox 3.08 (Brainard, 1997), Matlab (R2009a, The Mathworks, Natick, MA) and C/C++. fMRI data were analyzed using Brain Voyager QX version 2.8 (Brain Innovation, Maastricht, The Netherlands) and Matlab. Sound editing was performed with Adobe Audition version 1.5 software (Adobe Systems, San Jose, CA). Sound equalization was performed with filters provided by the headphone manufacturer (Sensimetrics, Malden, MA).

#### 4.3.1 Participants

Three blind, male echolocation experts (EE1-EE3) participated in the study. EE1 (age 44) was enucleated in infancy due to retinoblastoma and reports to have used echolocation for as long as he can remember. EE2 (age 44) had lost sight due to retinopathy of prematurity. He reports having begun using echolocation in

his early twenties, but did not practice echolocation between age 34 and 40 due to health reasons. He resumed using echolocation on a daily basis at age 40. EE3 (age 29) gradually lost sight from birth due to glaucoma, and had only bright light detection since early childhood. At the time of testing he was completely blind. EE3 reports that he has used echolocation techniques since age 12. At time of testing, each of the echolocation experts reported using click-based echolocation on a daily basis.

We also tested six control participants (three congenitally blind non-echolocators [BC1-BC3; two male, aged 36, 25, 38, respectively] and three sighted individuals [SC1-SC3; two male, aged 26, 29, 30, respectively]). Control participants reported no prior use of or training in echolocation prior to participation.

#### 4.3.2 Experimental Stimuli

##### 4.3.2.1 Sound Stimuli: Setup and Recording Procedure

All auditory stimuli were recorded in a Beltone Anechoic Chamber at the National Centre for Audiology in London, Ontario, Canada, measuring 5.5 m high × 7.0 m wide × 3.7 m deep, and equipped with a 125-Hz cutoff wedge system on the walls and ceiling. The chamber floor was covered in foam baffles. Ambient noise recordings indicated a background noise (i.e., “noise floor”) of 18.6 dBA.

Recordings of the entire session's audio were acquired via in-ear binaural omnidirectional microphones (Sound Professionals-TFB-2; “flat” frequency range 20–20,000 Hz) attached to a portable Edirol R-09 digital wave recorder (16-bit, stereo, 44.1-kHz sampling rate). Microphones were placed directly at the opening of the echolocators' left and right auditory canals and held in place by a soft rubber “horn-shaped” housing that conformed to the shape of the concha. During recording, participants held their head stationary and faced straight ahead.

Recordings were made separately with EE1, EE2, and EE3.



#### 4.3.2.2 Echolocation Sounds

Similar to our previous studies (Arnott et al., 2013; Thaler et al., 2011, Thaler et al., 2014), echo stimuli were created by making binaural recordings of echolocation clicks and subsequent echoes as each echolocating participant was presented with sound-reflecting surfaces that were made of different materials. Thus, echolocation recordings contained both clicks and the click echoes. The advantage of using binaural microphones is that the sounds are perceived to be externalized when played back over headphones (i.e. that they are occurring ‘out in the world’ as opposed to inside of the head). The recordings were made in the presence of one of three materials: a whiteboard, synthetic foliage, and a fleece blanket covered with a fencing material<sup>5</sup> (Figure 4.1A). The objects were large (sizes varied) and were designed to encompass the entire ‘scene’ (i.e. to provide no shape or edge information). The materials were suspended from a pulley system on the ceiling and were centered at ear-level for each participant. During recording, the participant was positioned approximately 45 cm away from the material and told to click at a comfortable pace (see Figure 4.1B). We also made recordings of the participants’ clicks in the absence of any material (i.e. theoretically echoless) to serve as a ‘no-material’ condition. For all recording conditions, the participant was inside of the anechoic chamber by himself with the door closed. Examples of click-echo pairings for each condition are shown in Figure 4.1A.

#### 4.3.2.3 Sound Editing

From each echolocator’s recordings, we took individual click-echo pairings to create three unique 10-second exemplars for each condition (whiteboard,

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<sup>5</sup> During the planning of the experiment, we presented the echolocators with a number of different materials and had them report on the material properties they perceived (we did not provide them with any information prior to presentation). The three materials used here were chosen because the echolocators indicated that the echoes were reflected from these materials were salient and also that they sounded very differently from each other. The echolocators described the whiteboard as sounding “hard, flat, and smooth”, the synthetic foliage as sounding “like foliage”, and the fleece blanket covered in fencing material as sounding “sparse”.

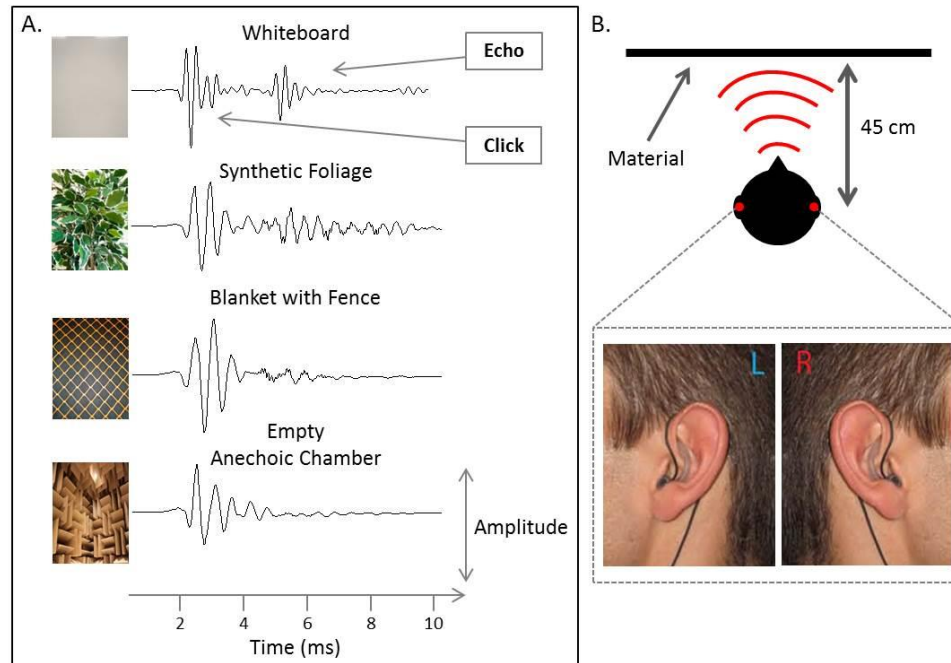


Figure 4.1. Material stimuli and setup for binaural recordings. A) Photos of the materials (and empty chamber) recording conditions, with sample waveforms for each condition (samples were extracted from EE1's recordings). B) The participant (EE1-EE3) was positioned approximately 45 cm from each material, which was suspended from the ceiling and was large enough to encompass the entire field and not provide shape or edge information. The participant wore binaural microphones (inset) and was told to click at a comfortable pace while the researchers recorded the clicks and returning echoes. For the empty anechoic chamber recordings no material was present and the participant was alone in the anechoic chamber. Recordings were made separately for EE1, EE2, and EE3.

synthetic foliage, fleece blanket covered in fencing material, and the empty chamber environment). This resulted in having three different sets of sound stimuli (i.e. from each echolocator's recordings), each including 12 sounds (4 conditions x 3 exemplars). Because the echolocators were free to click at their own pace, the number of click-echo pairings per 10-second stimulus varied within and between participants, with an average of 14 pairings per sound stimulus. The average acoustic energy of the sounds (in dB root mean square [RMS]) was -48.4 (SD = 1.9) for EE1, -46.1 (SD = 1.2) for EE2, and -45.9 (SD = 2.3) for EE3.

### 4.3.3 MRI Scanning

Imaging for all participants, except EE3, was performed at the Robarts Research Institute (London, Ontario, Canada) using a 3-Tesla, whole-body MRI system (Magnetom Tim Trio; Siemens, Erlangen, Germany) with a 32-channel head coil. EE3 was scanned at Durham University Neuroimaging Centre, James Cook Hospital, Middlesbrough, using the same model scanner and head coil.

#### 4.3.3.1 Setup and Scanning Parameters

Audio stimuli were delivered over MRI-compatible inset earphones (model S-14, Sensimetrics, Malden, MA). Participants adjusted the sound level to their own comfort. The earphones were encased in replaceable foam tips that provided 20- to 40-dB sound attenuation. Further sound attenuation was achieved by placing foam inserts between the head rest and the participants' ears. Due to the fact that the experiment involved listening to sound stimuli including faint echoes, the MRI's bore circulatory fan was turned off. A single-shot gradient echo-planar pulse sequence in combination with a sparse-sampling design (Hall et al., 1999) was used for functional image acquisition. Repetition time was 12 seconds (10-second silent gap + 2-second slice acquisition). The field of view was 211 mm with a 64 x 64 matrix size, which led to in-slice resolution of 3.3 x 3.3 mm. Slice thickness was 3.5mm and we acquired 38 contiguous axial slices covering the whole brain in ascending order. Echo time was 30 ms and flip angle was 78°.

#### 4.3.3.2 Anatomical Image

Anatomical images of the whole brain were acquired at a resolution of 1 x 1 x 1 mm using an optimized sequence (MPRAGE).

#### 4.3.3.3 Functional Paradigm

Each run contained silent baseline and experimental trials (Figure 4.2).

Experimental trials included a 10-second sound stimulus presentation (i.e. one of the four conditions [three materials and empty anechoic chamber]). Each sound presentation was followed by a 50-ms, 1200-Hz tone, which cued the participant to provide their response via button-press (Behavioural Paradigm below).

Functional scans began 10 seconds after the run had started and lasted 2 seconds. The next trial began immediately after scanning had ended. Silent baseline trials differed from experimental trials in that the 2-second functional scan occurred after 10 seconds of silence (which was not followed by the response-cue tone and participants did not make a button-press). The echolocating participants did not listen to their own click recordings, but rather to the recordings of one of the other echolocators (Behavioural Paradigm below). Stimulus presentation was pseudo-randomly ordered such that each run contained eight clusters, each cluster containing an exemplar of each of the four experimental conditions. The order of the four conditions was counterbalanced across clusters using a Latin square design. Each cluster of four conditions was preceded by a silent baseline trial, and each run began and ended with a silent baseline trial. Thus there were a total of 41 trials per run (9 silent + 8 x 4 experimental) and the durations of each run was 41 x 12 seconds. Each participant completed five runs.

#### 4.3.3.4 Behavioural Paradigm

As mentioned above, the echolocating participants did not listen to their own recorded clicks and echoes. The purpose of this was to account for the fact that recordings were not made with control participants and therefore they listened to the recordings of another individual. The participants assigned to each set of

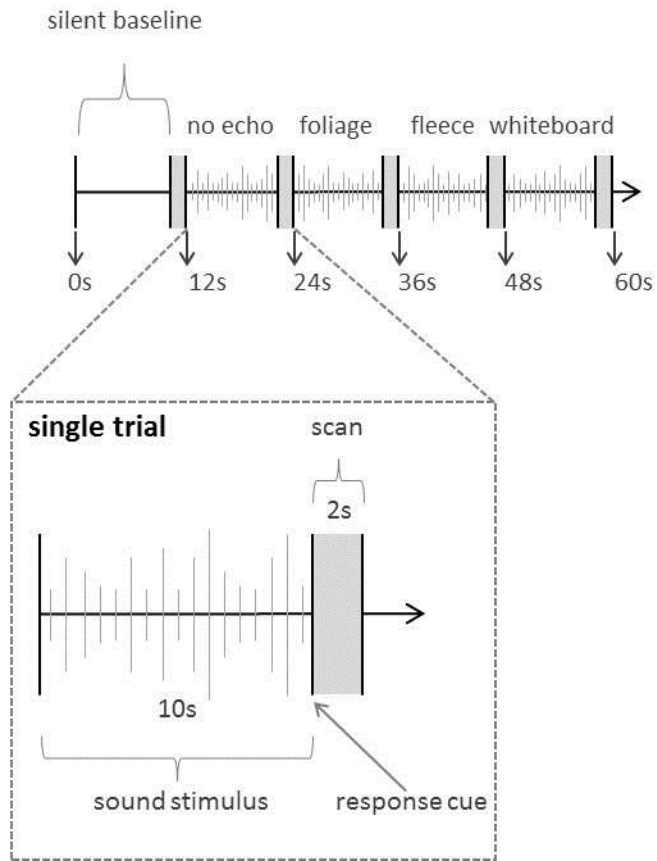


Figure 4.2. Experimental design. Time is indicated by the arrow from left to right in seconds (s). An enlarged view of a single trial is shown in the inset. The presentation of the material sounds was pseudo-randomized across runs, and the labeling in the top panel for each sound is for illustrative purposes only. Each sound presentation was followed by a ‘beep’ which cued the participant to respond via button-press. Every fifth trial was a silent baseline which was not followed by a ‘beep’ and participants did not provide a response. Functional slice acquisition took place only during the 2-second period between sound presentations.

recordings were as follows: EE1's recordings: EE3, BC3, SC3; EE2's recordings: EE1, BC1, SC1; EE3's recordings: EE2, BC2, SC2.

Participants were asked to keep their eyes closed during the duration of the experiment. The task was a 1-interval-4-alternative forced choice paradigm. The participant listened to the echolocation sound and judged the material properties of the sound reflecting surface (whiteboard, synthetic foliage, fleece blanket with fencing, no material [empty anechoic chamber]). Participants indicated their response with a button press using a four-button magnetic resonance-compatible keypad.

#### 4.3.3.5 Prior to MRI

**EXPERTS:** Before MRI scanning, the echolocating participants were familiarized with the sounds they would be listening to during experimentation. Feedback was provided initially to ensure that the participants were accurately identifying the echoes. A mock run was performed without feedback just prior to testing.

**BLIND AND SIGHTED CONTROL PARTICIPANTS:** Blind and sighted controls completed a 40-minute practice session to familiarize themselves with their respective echo stimuli. Feedback was provided for the first portion of the practice session until the participants could comfortably and reliably identify the sound stimuli. This portion of practice was followed by a mock run during which no feedback was provided. Just prior to MRI, participants were once again familiarized with the sounds and feedback was provided.

#### 4.3.4 fMRI Data Analysis

##### 4.3.4.1 Preprocessing and Coregistration

Each functional run began with three functional scans not saved to disk (scanner manufacturer default programming for functional sequences). Following these initial scans, functional data acquisition began. The first volume of each run was not included in the functional data analysis. Each run was subjected to slice scan time correction (tri-linear sinc), temporal high-pass filtering (cut-off at 2 sines/cosines) and three-dimensional motion correction (sinc). To align the

functional to the anatomical data for each participant, we first used three-dimensional motion correction to align each volume within a run to the functional volume closest to the anatomical scan. This volume was co-registered to the anatomical scan of that same participant. The anatomical for each participant was then transformed into standard stereotactic space (Talairach and Tournoux, 1988). Spatial smoothing was not applied to the data.

#### 4.3.4.2 Functional Analyses

Due to the nature of the study and the small number of participants, all analyses were performed on a single-subject level.

##### 4.3.4.2.1 BOLD Activity Related to Echolocation Stimulation Compared with Silence

To compare brain activity related to the processing of echolocation sounds as compared to a silent baseline for each participant, we ran a fixed-effects general linear model (GLM) with the stick-predictor 'All Sounds' to the z-transformed time courses of the runs (5 runs per participant; for EE3, the first run was omitted due to head movement-related artifacts). To determine where BOLD activity during sound-stimulation trials exceeded activity during silent baseline trials, we isolated voxels where the beta value of the 'All Sounds' predictor was significantly larger than zero. To control for Type-I error probability, each participant's data was subjected to a cluster threshold correction (Forman et al., 1996). Cluster threshold values were estimated in volume space using the BrainVoyager Cluster Threshold Estimator Plugin (Goebel et al., 2006) (see Supplemental Table S1). Following the cluster correction, individual data was also subjected to a false discovery rate (FDR) correction of  $p < .01$ .

##### 4.3.4.2.2 BOLD Activity Related to Material Echoes

The purpose of this analysis was to isolate the processing of only the echoes reflected from the materials. To obtain activity related to echo processing, we applied a fixed-effects GLM with the following contrast: (whiteboard + synthetic

Table 4.1.

*Summary of Participants' Behavioural Performance*

Performance on Material Discrimination Task (% correct)							
Participant	Whiteboard	Synthetic Foliage	Fleece-Fence	Empty Chamber	Overall Accuracy	Test Result	Significance
<b>EE1</b>	100	100	95	72.5	91.86	21.64	p < .001
<b>EE2</b>	92.5	92.5	85	67.5	84.38	19.19	p < .001
<b>EE3</b>	97.5	95	72.5	62.5	81.88	16.53	p < .001
<b>BC1</b>	50	33.3	55	45	45.83	6.61	p < .001
<b>BC2</b>	55	45	33.3	67.5	50.2	8.08	p < .001
<b>BC3</b>	55	57.5	70	92.5	68.75	14.125	p < .001
<b>SC1</b>	92.5	45	45	45	56.88	10.21	p < .001
<b>SC2</b>	37.5	37.5	45	45	41.25	5.14	p < .001
<b>SC3</b>	55	55	45	100	63.75	12.49	p < .001

Note: Test statistics and significance values are the result of binomial tests comparing each participant's overall percentage correct performance to chance (25%).



foliage + fleece with fence) > empty anechoic chamber. Again, each participant's data was subjected to cluster threshold correction (see Supplemental Table S1) and FDR correction of  $p < .05$ . A more liberal threshold was used for this contrast because the material-related activation (contrast all materials > silence) was not as robust.

## 4.4 Results

### 4.4.1 Behaviour

The participants' behavioural task during fMRI scanning was to identify the material of the sound-reflecting surface (i.e. whiteboard, synthetic foliage, fleece blanket with fencing, or no material [empty anechoic chamber environment]). The behavioural performance (as percent correct) for all participants is shown in Table 4.1. Each participant completed five runs (with the exception of EE3, for whom analyses were conducted on runs 2-5), with 40 trials in each run (10 repetitions per material condition), for a grand total of 200 behavioural trials. EE3 completed four runs and thus completed 160 behavioural trials. Binomial tests were conducted on each participant's overall percentage correct performance compared to chance (25%). The results of the binomial tests revealed that all participants performed significantly better than chance ( $p < .001$ ; Table 4.1). It is also evident that, even though each of our participants could perform the task, each of the echolocation experts had higher accuracy than any of the control participants. Recall that none of the participants – even the expert echolocators – listened to their own recordings. Thus, this difference in performance is due to echolocation expertise, rather than familiarity with the sounds.

### 4.4.2 BOLD Activity Related to Echolocation Stimulation Compared with Silence

Figures 4.3 and 4.4 show slice views of the expert echolocator's (Figure 4.3) and blind and sighted control participants' (Figure 4.4) BOLD activity associated with the processing of all of the sound stimuli compared to silence. The top row for each group of participants shows coronal slices (with Talairach y-coordinates indicated below). All participants showed highly significant activation in bilateral

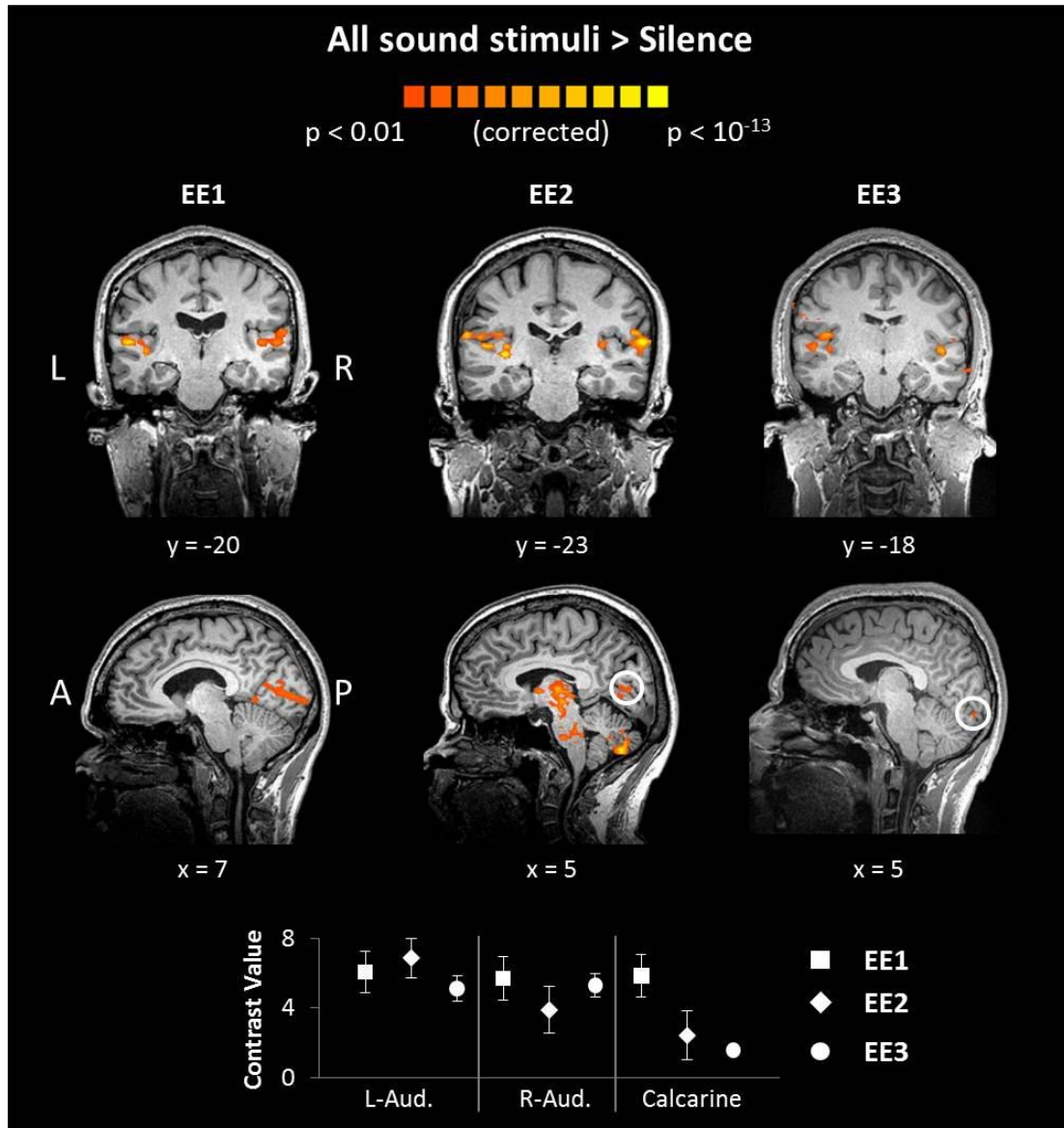


Figure 4.3. BOLD activation for participants EE1-EE3 related to echolocation stimulation compared with silence. The top row shows coronal slice views with activation in bilateral Heschl's gyrus for all three echolocating participants (with Talairach y-coordinates below). The bottom row shows sagittal slices views with activation in the right calcarine sulcus in all three participants (with Talairach x-coordinates below). The contrast values (with SE) for each region of activation are shown in the plot. EE1 exhibited three separate areas of activation along the calcarine sulcus, and the contrast value plotted represents the average of these three regions. Complete Talairach coordinates and sizes of all regions are shown in Table 4.2.

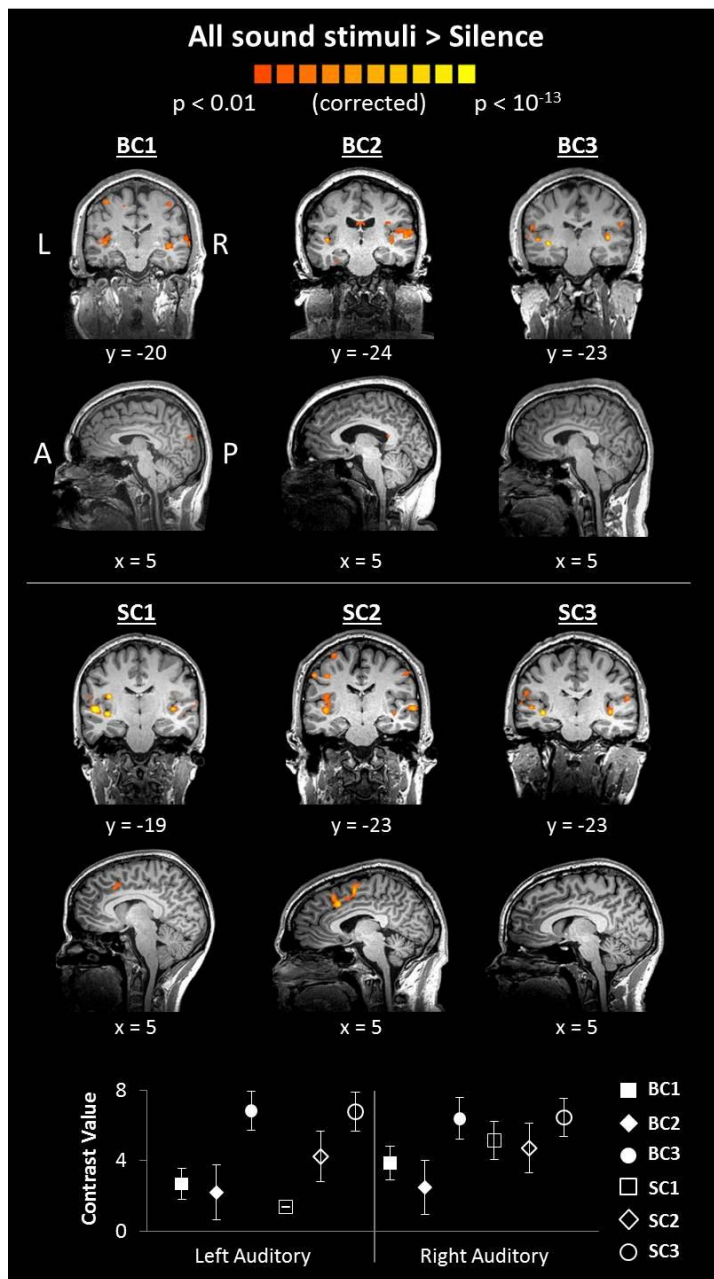


Figure 4.4. BOLD activation for blind (BC1-BC3) and sighted (SC1-SC3) control participants related to echolocation stimulation compared with silence. The top row for each group of participants shows coronal slice views with activation in bilateral Heschl's gyrus (with Talairach  $y$ -coordinates below). The bottom row for each group of participants shows sagittal slice views at the location of the right calcarine sulcus (which was activated in EE1-EE3; Talairach  $x$ -coordinates are below). Control participants did not exhibit any activation in this area. The contrast values (with SE) for each region of activation are shown in the plot. Complete Talairach coordinates and sizes of all regions are shown in Table 4.2.

Heschl's gyrus, which was expected given that Heschl's gyrus contains the primary auditory cortex. The average contrast values for each of the activated regions are shown in the plot at the bottom of each figure, and the Talairach coordinates and sizes of each region are shown in Table 4.2 for all participants.

The bottom row in Figure 4.3 and in each participant section in Figure 4.4 shows sagittal slice views (with Talairach *x*-coordinates indicated below) for each participant. The contrast revealed activation along the right calcarine sulcus, but only in the three echolocating participants. In particular, EE1 showed activation along the entire sulcus, while EE2 and EE3 showed smaller isolated areas of activity. Previous research on the blind has shown that auditory stimulation in the blind brain can activate what are considered 'visual' brain areas in the sighted brain (for review, see Bavelier & Neville, 2002; Merabet & Pascual-Leone, 2010). Interestingly, though, the blind control participants did not exhibit significant activation in the occipital cortex in our experiment, even at more liberal thresholds (although BC1 shows a small region of activation at the parieto-occipital junction). This absence of occipital activation in the blind control participants in response to auditory stimulation is addressed in the Discussion. Sighted controls also did not show calcarine activation, even at more liberal thresholds. The average contrast values for each of the activated regions are shown in the plot at the bottom of each figure, and the Talairach coordinates and sizes of each region are shown in Table 4.2 for all participants.

#### 4.4.3 BOLD Activity Related to Material Echoes

Figure 4.5 shows the BOLD activity associated with the processing of only the material echoes. As described in the methods, we isolated the echoes by subtracting the activity related to the click-only empty anechoic chamber condition from the activity related to the three click-echo material conditions. This contrast revealed similar but not overlapping areas of activation within the region of the left parahippocampal cortex (an area encompassing the parahippocampal gyrus, fusiform gyrus, and anterior CoS) in all three expert echolocators. The relative location of each echolocator's region of activation is shown on an



Table 4.2.

*Center-of-gravity coordinates (Talairach space) and sizes of activated regions within auditory, calcarine, and parahippocampal cortex.*

All Sound Stimuli > Silence (p < .01)						All Sound Stimuli > Silence (p < .01)					
Auditory Cortex Activation						Calcarine (visual) Cortex					
Subject	Hemi.	No. Voxels	x	y	z	Subject	Hemi.	No. Voxels	x	y	z
EE1	Left	233	-41	-20	3	EE1	Right-1	288	7	-95	3
	Right	298	43	-20	9		Right-2	432	7	-83	6
EE2	Left	559	-35	-20	3		Right-3	555	10	-77	9
	Right	320	37	-26	3	EE2	Right	371	5	-77	6
EE3	Left	496	-50	-20	3	EE3	Right	340	1	-92	6
	Right	220	46	-14	0						
BC1	Left	294	-41	-20	3	All Materials > Empty Chamber (p < .05)					
	Right	362	40	-20	0	Parahippocampal Cortex					
BC2	Left	316	-44	-23	3	Subject	Hemi.	No. Voxels	x	y	z
	Right	372	37	-26	6	EE1	Left	25	-14	-55	-6
BC3	Left	261	-38	-23	0	EE2	Left	278	-20	-53	-9
	Right	219	38	-22	3	EE3	Left	56	-11	-53	-6
SC1	Left	326	-38	-17	-3						
	Right	301	37	-20	3						
SC2	Left	562	-41	-20	0						
	Right	215	37	-26	-1						
SC3	Left	216	-38	-23	0						
	Right	247	37	-23	6						

averaged brain in the magnified inset in Figure 4.5 (the Talairach coordinates and sizes of each region are shown in Table 4.2). Interestingly, Arnott et al.'s (2008) findings on visual and auditory material processing in sighted individuals also revealed parahippocampal cortex activation, but their participants showed activation in the right hemisphere. This difference in lateralization is addressed in the Discussion. The bottom panel of Figure 4.5 shows the left parahippocampal cortex of each of the blind and sighted control participants, none of whom showed any significant activation within that region, even at more liberal thresholds ( $p < 0.1$ ). It is noteworthy that none of our participants showed activity in Heschl's gyrus, or in calcarine cortex, for this contrast.

Activation within the left parahippocampal cortex was consistent across EE1, EE2, and EE3, but activity was also seen in other areas, most notably for participant EE1. EE1 exhibited bilateral activation within the cingulate cortex and middle temporal gyrus, as well as small regions of activation within the medial parietal cortex, prefrontal cortex, and cerebellum. Because these areas of activation were present in only one echolocating participant, our discussion will focus primarily on the consistent PHC activation in all echolocators.

## 4.5 Discussion

Previous neuroimaging research in blind human echolocators has provided evidence for a functional role of calcarine cortex in processing echoes reflected from silent objects (Thaler et al., 2011). More recent research (Arnott et al., 2013; Thaler et al., 2014) has suggested that this occipital activation is likely not due to general cross-modal plasticity, but rather that the functional nature of particular visual brain areas (such as the LOC, or MT+) are preserved. In other words, the processing of echoes may show feature-specificity similar to the normal functions of such brain areas for the processing of vision. Given the evidence for feature-specific activation, the aim of the current experiment was to determine how the blind echolocating brain processes echoes reflected from surfaces of different materials. In particular, we were motivated by findings about visual (Cant & Goodale, 2007, 2010; Cavina-Pratesi et al., 2011; Hiramatsu, Goda, & Komatsu,

2011; Jacobs, Baumgartner, & Gegenfurtner, 2014) and visuo-auditory (Arnott et al., 2008) material processing that implicated CoS and PHC. Our results revealed activation in left parahippocampal cortex for all three echolocating participants.

By showing material related activity in PHC, our results suggest that material processing through echoes may recruit the same general regions of PHC that have been implicated in both visual and auditory processing of material properties (Arnott et al. 2008; Cant & Goodale, 2011; Jacobs, Baumgartner, & Gegenfurtner, 2014). We saw no activation, however, in posterior regions of CoS that have also been associated with aspects of the visual processing of material. A discrepancy between our and Arnott et al.'s (2008) findings is that Arnott et al. observed activation in the right hemisphere whereas we show activation only in the left hemisphere across all three echolocators. This difference could potentially be attributed to the fact that our stimuli were specifically designed to minimize any spatial information (i.e. the material encompassed the whole 'scene' and had no discernible edges/boundaries for the echolocators), whereas the stimuli in Arnott et al.'s study had inherent spatial properties (for example, the sound of a snack food bag could elicit spatial imagery of the object's form, or the object being spatially manipulated). The right-lateralized material-related activation found previously could then be due in part to the spatial properties of the stimuli. In fact, right occipital regions in the blind have been shown to be preferentially activated for spatial versus non-spatial stimuli in both the auditory and tactile domains (Collignon et al., 2011; Renier et al., 2010). Nevertheless, future research is needed to follow up on these differences in lateralization.

One could argue that the observation of PHC activity in only the blind echolocating participants (and not in blind or sighted controls) could be due simply to general echo expertise and not functionally specific to material perception, particularly considering that the echolocating participants showed considerably higher behavioural performance than the control participants. Sighted participant SC1, though, showed comparable performance to the expert echolocators in identifying the 'whiteboard' echoes. In a contrast isolating the processing of just the whiteboard echoes, however, we found no evidence of



PHC activity in this participant, even when using liberal, uncorrected statistical thresholds. Furthermore, considering that the PHC has previously been implicated in material processing in other perceptual domains (vision and audition), we are more confident in attributing the activation found in the current study to material-echo perception. Nevertheless, future research should aim to disentangle the possibilities of expertise versus feature-specific activation in expert echolocators.

The observation of activation within the PHC invites speculation about the nature of the activity we found, particularly because of PHC's typical (though not exclusive) association with scene perception (for review, Aminoff, Kveraga, & Bar, 2013). Specifically, in our study the presence of a material could also be considered the presence of a particular material surface, or 'scene' respectively, so that one could argue that the PHC activation we found represents echo-scene related activation, rather than echo-material related activation. In previous work, however, which aimed to determine echo-scene related activation within blind echolocators (Arnott et al., 2013) we found results suggesting involvement of auditory and calcarine cortex rather than PHC. Nevertheless, it will be important for future research on material perception via echolocation to further disentangle the possible explanations for the PHC activation we found.

In sum, our results are most similar to those obtained by Arnott et al., (2008). Most importantly, the fact that we found highly consistent activation in left PHC in all three echolocating participants, in combination with those previous findings, suggests the potential involvement of visuo-auditory material processing areas in PHC for processing of material echoes in blind experts.

In addition to the main findings in parahippocampal cortex, we also observed activation along the right calcarine sulcus in all echolocating participants, but this activation was observed only for the contrast isolating activity related to echolocation stimulation compared to silence. This lateralization is consistent with previous findings on calcarine activation in human echolocators (Thaler et al., 2011) and also with general auditory stimulation in the blind (e.g., Weeks et al., 2000). Surprisingly, we did not observe calcarine

activity in our blind control participants, even when applying more liberal statistical thresholds. Because we have not tested this set of blind control participants on any other auditory tasks, we cannot say whether the absence of occipital activation in this case is related to the participants themselves (i.e. they do not show occipital activation for any auditory tasks) or whether it is something related to the echolocation task. Future research should address this.

Interestingly, we did not observe calcarine activity in the echolocating participants for the contrast (all materials > empty chamber). Since this contrast isolated processing of echoes (which in our study were always material echoes), the absence of calcarine recruitment for this contrast seemingly runs counter to what we have found previously (Thaler et al., 2011). A difference between the current and our previous study, though, is that the material-echoes in the current study were designed with the goal to convey material information per-se, i.e. to minimize spatial information. Thus, again, one could argue that the material echoes in our study did not contain a spatial component, and it is possible that the calcarine activation previously associated with echo perception was particularly related to the spatial components of the echoes (Thaler et al., 2011). Based on the idea that echo-related activation in calcarine cortex is tied to the spatial component of echoes, we would expect that contrasts of various sorts of spatial echo-information should lead to differences in activation in calcarine cortex. Remarkably, this is exactly what we found when we reported modulation of echo-related activity in calcarine cortex with echo laterality (Thaler et al., 2011) and eccentricity (Arnott et al., 2013). Thus, these findings suggest the viability of the idea that echo-related activity in calcarine cortex of blind experts is tied to the spatial component of the echoes. An alternative, though not mutually exclusive, explanation for the absence of calcarine activity for the contrast (all materials > empty chamber) in our study is the idea that the recruitment of calcarine cortex in the case of material-echo perception is unnecessary due to the fact that the PHC is normally recruited for the processing of material properties within the auditory (and visual) domain. Future research should address these possibilities.

Because echolocation is an auditory process, it must involve auditory processing. Yet, for the contrast (all materials > empty chamber) we were unable to find significant differential activity in primary auditory cortical areas, i.e. Heschl's gyrus. The lack of any difference in activity in auditory cortex for the contrast between (all materials > empty chamber) was expected, because we had created stimuli so that the acoustic differences were minimal and the only difference was the presence or absence of very faint echoes. It is possible, therefore, that the auditory processing of the very faint echoes did not yield a significant differential BOLD signal in primary auditory areas because activity in those areas might have been dominated by the processing of the much louder and more salient clicks (which are present in both material and empty chamber sounds).

Given the possibility of a multimodal material processing area within PHC, one must also consider the perception of material properties via haptics. Research on sighted individuals has, not surprisingly, shown activation within the somatosensory cortex (such as the postcentral gyrus, parietal operculum, and insula) related to the tactile exploration of objects with different material or texture properties (Podrebarac, Goodale, & Snow, 2014; Servos, Lederman, Wilson, & Gati, 2001; Stilla & Sathian, 2008). Furthermore, haptic texture-related activation has been observed within the medial occipital cortex (MOC), with regions of activity overlapping (Stilla & Sathian, 2008) or adjacent to (Podrebarac et al., 2014) visual-texture selective areas. Interestingly, though, the visuo-haptic texture-selective areas within MOC are quite different from the visuo-auditory material area in right PHC found by Arnott et al. (2008), and from the areas within left PHC observed in the current study. In the blind, material perception has been investigated only in the tactile domain, but not in the auditory domain. With regard to tactile perception of materials, no notable differences in behavioural performance have been reported to date between sighted and blind people (Grant, Thiagarajah, & Sathian, 2000; Heller, 1989), with the exception of Braille patterns which might be related to blind people's Braille proficiency (e.g., Grant, Thiagarajah, & Sathian, 2000). To the best of our knowledge, at present there is

no study having investigated brain areas involved in tactile perception of materials per se in the blind (i.e. not the perception of Braille or dot position offset). In sum, it will be important for future research to address how the blind and sighted brain processes material-related information from the echolocation, pure auditory, and tactile domains.

#### 4.5.1 Conclusions

The aim of the current study was to investigate the neural correlates of material processing through echolocation in blind human expert echolocators. The perception of material has real-world implications for blind individuals, with immediate benefits for navigation, orientation, and obstacle avoidance. Given the evidence suggesting that the blind echolocating brain may show functional specificity for echoes in a way similar to visual processing, we aimed to determine whether material processing via echoes would make use of brain areas normally associated with such functions in vision. Our results indicated that the processing of material-echoes makes use of an area within the parahippocampal cortex that has previously been implicated in both visual and auditory material processing. Future research should draw direct comparisons between material processing through echolocation, 'regular' hearing, and vision.

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Chapter 5:  
General Discussion



## 5.1 Summary of Findings

The goal of the current thesis was to better understand some of the basic functions of human echolocation. Specifically, I used behavioural psychophysical techniques to examine the ability of human echolocators to determine the shape and size of objects and I used neuroimaging to observe the neural correlates of material-echo processing. The following will summarize the main findings of this thesis.

In Chapter 2, I showed that six expert echolocators could discriminate between four different two-dimensional shapes (a square, triangle, horizontally-oriented rectangle, and vertically-oriented rectangle) with remarkable precision, but that their ability to do so was dependent on the use of head and body movements. When the echolocating participants were instructed to remain still, we observed a substantial decrease in performance. We suggested, then, that these movements allowed the echolocators to scan and trace the edges of the objects, with each echo providing a ‘snapshot’ of information about the location from which it was reflected. By piecing-together each of these snapshots, the echolocator could produce an overall percept of the object’s shape. This process of combining small pieces of information is strikingly similar to how sighted individuals perceive objects and scenes (although echolocation certainly operates on a much cruder scale than vision). Therefore, we suggested that these movements may be similar to the many saccadic eye movements used for visually surveying an object or scene.

In Chapter 3 I investigated whether or not a blind expert echolocator shows size constancy for object size perception. Recall that size constancy is a visual-perceptual principle, and refers to the stable perception of object size at various distances, despite the fact the retinal image size is directly affected by distance. The results in Chapter 3 indicated that the expert echolocator indeed showed size constancy, even though changes to the distance of the objects had a direct effect on size-related echo information. These findings are intuitive considering that in order to successfully navigate one’s surroundings based on echoes the information content must be accurate. And, of course, we know

anecdotally and from the existing literature on human echolocation that blind expert echolocators can accurately and reliably perceive and navigate their surroundings via the information content of echoes. The work presented in Chapter 3, though, was the first to directly test and confirm that size constancy operates via echolocation.

In Chapter 4 I used functional neuroimaging to examine the neural correlates of material processing in echolocation. Material information contained in echoes is informative for navigation and obstacle avoidance, and the broadband echolocation signals used by human echolocators are well-suited for discriminating material properties. The results of this project demonstrated not only that expert echolocators can discriminate between recorded echoes reflected from different materials, but also that the processing of these echoes was associated with activity within the parahippocampal cortex. This area has been previously implicated in the processing of visual and auditory material properties. These findings support the suggestion that echo-related neural activity in visual cortical areas shows feature-specificity similar to related functions in vision.

## 5.2 Implications for the Blind

### 5.2.1 General Benefits

The work presented in the current thesis – along with much of the existing work in the human echolocation literature – supports echolocation as a viable resource for the blind. The research reported here and elsewhere demonstrates that the information these blind individuals can extract from echoes is an accurate representation of objects and surfaces in the real world, and thus this information can be relied upon for navigation, obstacle avoidance, and general perception. Furthermore, as mentioned throughout this thesis, echolocation allows for the detection and perception of silent objects at a distance, and thus provides a unique perceptual opportunity that would otherwise not be available to blind individuals (that is, without the use of echolocation or a sensory substitution device).

Although the current thesis emphasized the relationship between echolocation and vision, it is important to note that echolocation is an extraordinary and valuable skill on its own, regardless of any connection with vision or other sensory modalities. Furthermore, the fact that echolocation is a teachable skill means that it is theoretically available to anyone – blind or sighted – and can offer perceptual benefits above and beyond the traditional senses. In terms of the blind population, in addition to the benefits discussed throughout this thesis, there is evidence suggesting that the use of echolocation improves auditory space representations, and that some blind echolocators even perform superiorly to sighted people (Vercillo, Milne, Gori, & Goodale, under review). In a more general sense, echolocation expertise has been positively correlated with higher salary and greater mobility in unfamiliar places as compared to blind individuals who do not echolocate (Thaler, 2013). Given the obvious benefits of echolocation, research should continue to validate its utility in hopes of having echolocation training become more ubiquitous in the blind (and even the sighted) community.

### 5.2.2 Echolocation devices

Substantial efforts have been made in research and engineering to create sensory substitution devices (SSDs) to allow blind individuals to ‘see’ via the remaining senses, such as audition or touch (Bach-y-Rita & Kercel, 2003; Proulx, Brown, Pasqualotto, & Meijer, 2012). Visual-to-auditory SSDs typically involve the use of a camera that scans an object or scene and then converts the visual information into an auditory signal. For example, sounds of different frequencies, intensities, and durations can be used to represent the location of objects in the scanned image. Similarly, visual-to-tactile SSDs convert visual information into a tactile signal that can be transmitted to the skin on the hand (Zelek, Bromley, Asmar, & Thompson, 2003), tongue (Bach-y-Rita, 2004) or other areas. Similar to the results on echolocation and other auditory-related tasks activating visual cortical areas, the use of SSDs has been found to activate the occipital cortex in

the blind (Amedi et al., 2007; Collignon, Lassonde, Lepore, Bastien, & Veraart, 2007; DeVolder et al., 1999).

Although the research is promising and many of the devices are successful, the use of a device can be inconvenient and unpleasant. Echolocation, on the other hand, has a unique benefit in that no device is required at all. The fact that there is no device required also means that there is no cost, maintenance, power requirements, etc. associated with the use of echolocation, and thus it is a resource available to all (although training is recommended). Furthermore, the use of a self-produced signal and its echo may allow for efference copy mechanisms to operate and make precise comparisons between the outgoing and incoming signals. The fact that the echolocation involves the emission of a self-produced signal also allows the individual to easily modify the signal to best suit the demands of particular tasks and environments, although research has not been done to verify or quantify this as of yet. This is not to say that SSDs are not effective, though. In fact, visual-to-tactile-SSDs, for example, may be particularly useful for those with poor hearing. For example, overall hearing sensitivity as well as relative sensitivity between each of the ears tends to deteriorate with age, and thus older individuals may benefit from the use of tactile SSDs as opposed to echolocation. Overall, the use of any device or technique that improves and enriches the daily lives of blind individuals should be fully supported.

### 5.3 Future Directions

As mentioned throughout this thesis, research on human echolocation is lacking and thus our understanding is limited, particularly in comparison to the literature on echolocating animals such as bats and dolphins. A benefit of this limited understanding, though, is that the possibilities for future research on human echolocation are seemingly endless. The following will outline some potential avenues for future research that stem from the findings presented in this thesis.

In Chapter 2 I demonstrated that the use of head movements to ‘scan’ the objects’ edges was required for successful shape discrimination. An obvious and

logical next step, then, is to investigate these movements in greater detail. For example, how do the head movements interact with other variables such as distance and how do these interactions affect echo content and perception? Furthermore, it would be interesting for future research to investigate head movements in more real-world contexts. In Chapter 2, the participants had prior knowledge of the objects before performing the task (they were given the opportunity to haptically explore the objects). In a future investigation, one could use a motion-tracking system to study how expert echolocators use head and body movements in naïve situations; for example, one could have an echolocating participant locate and identify a goal object within an unfamiliar environment. Motion-tracking could shed light on the different types of movements used when searching for an object versus identifying an object. These processes have been investigated to some extent in the context of bat echolocation, and researchers have demonstrated that bats use large scanning movements when exploring a scene and use smaller, more detailed movements when examining an object or obstacle (Hardiess, Gillner, & Mallot, 2003; Rayner, 1998; Seibert, Koblitz, Denzinger, & Schnitzler, 2013). It would be interesting to see if human echolocators show similar scanning behaviours for such tasks.

A number of studies have shown that sighted people can learn to perceive object features via echoes (e.g., Hausfield, Power, Gorta, & Harris, 1982; Schenkman & Nilsson, 2010; Teng & Whitney, 2011; Wallmeier, Geßele, & Wiegrebe, 2013), and obviously blind individuals can learn this technique as well. This presents an interesting opportunity to train individuals to use echolocation and examine the behavioural and neural changes associated with training and acquisition of the technique. Furthermore, if training is provided to individuals of various ages, one could make inferences about neuroplasticity and sensitive periods of development by tracking functional and structural cortical changes associated with echolocation training. An investigation of this kind would not only be beneficial in terms of making a scientific contribution, but also simply in terms of providing a new perceptual resource to blind and/or sighted individuals.

In Chapter 3, I showed that an expert echolocator shows size constancy for objects perceived via echoes. These results present an interesting opportunity to further investigate size constancy in blind echolocators with the use of functional neuroimaging. A recent neuroimaging study investigating size constancy in the context of visual afterimages found that activation in primary visual cortex was correlated with the perceived size of the afterimage and not the retinal image size (Sperandio, Chouinard, & Goodale, 2012). Given that size constancy also applies to object size perception in echolocation and the fact that echo stimuli tend to activate primary visual cortex in blind individuals, it would be interesting to see whether this activation reflects the perceived size of objects or the raw size information contained in the echoes. An investigation of this type could shed light on potential top-down modulatory mechanisms that influence the processing and ultimately the perception of the information contained in echoes.

Given some of the limitations in the work presented in Chapter 4, future research should aim to better understand how the echolocating brain processes the material properties of echo-reflecting surfaces. Considering that material information in echoes is based on frequency composition (relative to the emitted signal), future research should aim to determine if material-related activity in the brain is modulated by the frequency content of echoes (which is indicative of the material properties of the echo-reflecting surface). Furthermore, one could investigate whether or not a correlation exists between the frequency composition of the echoes and the associated neural activity. For example, using multi-voxel pattern analysis (MVPA), one could determine whether different patterns of activity underlie the processing of different classes of material properties. Overall, having a better understanding of material processing in echolocation – as well as various other object features contained in echoes – could potentially contribute to methods and strategies that can optimize echo content.

The above-mentioned suggestions for future research are only a select few of the vast number of possibilities in the study of human echolocation. Even with our limited current understanding, the recent research in the field is certainly

encouraging, and the future of human echolocation research is sure to present exciting and significant contributions.

## 5.4 Conclusions

The work presented in this thesis represents original and significant findings related to the perception of shape, size, and material properties by blind individuals who use echolocation. Not only do these findings highlight some of the impressive perceptual abilities afforded by echolocation, but they also shed light on the numerous similarities between vision and echolocation, suggesting further parallels between the two modalities than previously recognized. Furthermore, the results of the current projects inspire several potential avenues for future research on human echolocation. Taken together, the findings presented in this thesis represent a strong and meaningful contribution to the scientific understanding of human echolocation.

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## Appendix A: Supplemental Information for Chapter 4

Supplemental Table S1.

Cluster size threshold values (in mm<sup>3</sup>) for all participants and for each contrast.

Participant	Contrast	
	All sounds > silence (p < .01)	All materials > empty chamber (p < .05)
EE1	212	108
EE2	178	133
EE3	183	113
BC1	272	208
BC2	206	117
BC3	198	188
SC1	208	186
SC2	241	194
SC3	201	199

## Appendix B: Copyright Permissions

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Best regards,

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East, Deborah

to Jennifer

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Our Ref: DE/NNCS/P1325

3<sup>rd</sup> June 2014

Dear Jennifer Milne,

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**A blind human expert echolocator shows size constancy for objects perceived by echoes – Neurocase: The Neural Basis of Cognition – Authors – Jennifer L. Milne, Mimma Anello, Melvyn A. Goodale & Lore Thaler.**

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# Appendix C: Ethical Approval



## Use of Human Participants - Ethics Approval Notice

**Principal Investigator:** Dr. Mel Goodale  
**Review Number:** 06882E  
**Review Level:** Delegated  
**Approved Local Adult Participants:** 500  
**Approved Local Minor Participants:** 0  
**Protocol Title:** The neural substrates of visual perception & visually-guided actions in neurological patients.  
**Department & Institution:** Schulich School of Medicine and Dentistry/Physiology & Pharmacology, University of Western Ontario  
**Sponsor:**  
**Ethics Approval Date:** March 22, 2012      **Expiry Date:** March 31, 2017  
**Documents Reviewed & Approved & Documents Received for Information:**

Document Name	Comments	Version Date
Revised Study End Date	The study end date has been extended to March 31, 2017 to allow for continuation of the project.	

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada ICH Good Clinical Practice Practices: Consolidated Guidelines, and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the University of Western Ontario Updated Approval Request Form.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.

The Chair of the HSREB is Dr. Joseph Gilbert. The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.



Ethics Officer to Contact for Further Information

Juanice Sutherland	Grace Kelly	Shantel Walcott
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*This is an official document. Please retain the original in your files.*

The University of Western Ontario  
Office of Research Ethics



Office of Research Ethics  
[Redacted]  
University of Western Ontario

August 5, 2009

*RE: Ethics number 06882E*

To Grace Kelly:

The purpose of this letter is to request that Jennifer Milne, a new graduate student be added as a co-investigator to our on-going research project entitled, "The Neural substrates of visual perception and visually-guided actions in neurological patients".

If you require any further information regarding this matter please do not hesitate to contact me.

Sincerely,



Melvyn A. Goodale, Ph.D., F.R.S.C.  
Canada Research Chair in Visual Neuroscience  
Distinguished University Professor  
Director, Centre for Brain and Mind



**Office of Research Ethics**

The University of Western Ontario



**Use of Human Subjects - Ethics Approval Notice**

**Principal Investigator:** Dr. M.A. Goodale

**Review Number:** 06882E

**Revision Number:** 13

**Review Date:** August 12, 2009

**Review Level:** Expedited

**Protocol Title:** The neural substrates of visual perception & visually-guided actions in neurological patients.

**Department and Institution:** Psychology, University of Western Ontario

**Sponsor:**

**Ethics Approval Date:** August 12, 2009

**Expiry Date:** March 31, 2012

**Documents Reviewed and Approved:** Revised study team.

**Documents Received for Information:** *Mina*

This is to notify you that The University of Western Ontario Research Ethics Board for Health Sciences Research Involving Human Subjects (HSREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the Health Canada/ICH Good Clinical Practice Practices: Consolidated Guidelines; and the applicable laws and regulations of Ontario has reviewed and granted approval to the above referenced revision(s) or amendment(s) on the approval date noted above. The membership of this REB also complies with the membership requirements for REB's as defined in Division 5 of the Food and Drug Regulations.

The ethics approval for this study shall remain valid until the expiry date noted above assuming timely and acceptable responses to the HSREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

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- b) all adverse and unexpected experiences or events that are both serious and unexpected;
- c) new information that may adversely affect the safety of the subjects or the conduct of the study.

If these changes/adverse events require a change to the information/consent documentation, and/or recruitment advertisement, the newly revised information/consent documentation, and/or advertisement, must be submitted to this office for approval.

Members of the HSREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the HSREB.



Chair of HSREB: Dr. Joseph Gilbert

Ethics Officer to Contact for Further Information			
<input type="checkbox"/> Janice Sutherland	<input type="checkbox"/> Elizabeth Wambolt	<input checked="" type="checkbox"/> Grace Kelly	<input type="checkbox"/> Denise Grafton

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LHRI

# Curriculum Vitae

## Jennifer Milne

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**Date of Birth:** June 4<sup>th</sup>, 1987

**Nationality:** Canadian

---

### Employment History

- 1/2014 – 4/2014**      **Graduate Teaching Assistant**  
Undergraduate Course: Introduction to Sensation and Perception  
Department of Psychology, The University of Western Ontario  
London, Ontario, Canada
- 9/2009 – 4/2010**      **Graduate Teaching Assistant**  
Undergraduate Course: Research Methods & Statistical Analysis  
Department of Psychology, The University of Western Ontario  
London, Ontario, Canada
- 1/2009 – 8/2009**      **Research Assistant**  
The Brain and Mind Institute  
Department of Psychology, The University of Western Ontario  
London, Ontario, Canada  
**Supervisor:** Dr. Melvyn A. Goodale

### Education

- 2011 – 2014**      **Ph.D. Candidate in Neuroscience**  
Graduate Program in Neuroscience,  
The Brain and Mind Institute, The University of Western Ontario  
London, Ontario, Canada  
Thesis: Seeing with sound: Investigating the behavioural  
applications and neural correlates of human echolocation  
**Supervisors:** Dr. Melvyn A. Goodale, Dr. Lore Thaler (Durham  
University, UK)
- 2009 – 2010**      **M.Sc. in Neuroscience**  
Graduate Program in Neuroscience,  
The Brain and Mind Institute, The University of Western Ontario  
London, Ontario, Canada  
**Thesis:** Effects of object connectedness on rapid visually-guided  
reaching to multiple goals  
**Supervisor:** Dr. Melvyn A. Goodale



2005 – 2009

**B.A.Hons in Psychology, graduated with distinction**

Minor in Political Science

Brescia University College, The University of Western Ontario  
London, Ontario, Canada

Thesis: Simultaneous encoding of target locations: The effect of multiple potential targets on pointing trajectories

**Supervisors:** Dr. John B. Mitchell, Dr. Melvyn A. Goodale

## Honours and Awards

5/2014

**Abstract Award**

(€200)

Workshop on Concepts, Actions, and Objects, Rovereto, Italy

5/2011

**Alexander Graham Bell Canada Graduate Scholarship**

(\$105,000 over 3 years)

Natural Sciences and Engineering Research Council of Canada

5/2011

**Ontario Graduate Scholarship**

(\$15,000 over 1 year -- declined)

Ontario Ministry of Training, Colleges, and Universities

5/2010

**Alexander Graham Bell Canada Graduate Scholarship**

(\$17,500 over 1 year)

Natural Sciences and Engineering Research Council of Canada

5/2010

**Ontario Graduate Scholarship**

(\$15,000 over 1 year -- declined)

Ontario Ministry of Training, Colleges, and Universities

5/2010

**Nominated for Graduate Student Teaching Award**

The University of Western Ontario, Canada

5/2009

**Undergraduate Student Research Award**

(\$4000 over four months)

Natural Sciences and Engineering Research Council of Canada

10/2007

**Dr. Pat Devolder Psychology Award**

(\$250)

Awarded to the student with the highest average in Psychology  
Brescia University College, The University of Western Ontario  
London, Ontario, Canada

10/2006

**Political Science Award**

(\$250)

Awarded to student with highest average in Political Science  
Brescia University College, The University of Western Ontario  
London, Ontario, Canada

9/2005

**Sister Mary Agnes Feurth Continuing Scholarship**

(\$10,000 over four years)

Awarded to the student with the highest incoming average  
Brescia University College, The University of Western Ontario  
London, Ontario, Canada

## Teaching Experience

### Undergraduate Teaching Assistant

- Introduction to Sensation and Perception
  - (2<sup>nd</sup> year undergraduate course, 1/2014 – 4/2014)
  - Guest Lecturer – presentation on human echolocation
- Research Methods and Statistical Analysis
  - (2<sup>nd</sup> year undergraduate course, 9/2009 – 4/2010)
  - Nominated for Graduate Student Teaching Award

### Supervision and Mentoring

- **Caitlin Byrne:** lab volunteer (February 2012 – August 2012) and research assistant (September 2012 – August 2013)
- **Mimma Anello:** undergraduate honours project in Physiology and Pharmacology at The University of Western Ontario (September 2012 – April 2013)
- **Ashley Gaw:** undergraduate honours project in Physiology and Pharmacology at The University of Western Ontario (September 2010 – April 2011)
- **Maria Khami:** undergraduate honours project in Physiology and Pharmacology at The University of Western Ontario (September 2009 – April 2010)

## Outreach, Media Interviews, and Community Service

Organizing committee, London Brain Bee Highschool Neuroscience Competition, 2014

Interviewed for CBC Radio program Quirks and Quarks, February 2013

Organizing committee, London Brain Bee Highschool Neuroscience Competition, 2013

Discussant, Blindsighted (Accessible Media television program), November 2012

Discussant, Accessible Media Radio Program, November 2012

Interviewed for Reader's Digest article "Bat Man", published in June 2012 issue

Discussant, NHK Television Documentary on Human Echolocation, June 2011

Discussant, Out of Their Minds (CBC Radio podcast), June 2011

Organizer, London Brain Bee Highschool Neuroscience Competition, 2011

Organizer, London Brain Bee Highschool Neuroscience Competition, 2010

## Publications

Vercillo, T., **Milne, J.L.**, Gori, M., & Goodale, M.A. Enhanced auditory spatial localization in blind echolocators. (in preparation)

Buckingham, G., **Milne, J.L.**, Byrne, C.M., & Goodale, M.A. The size-weight illusion induced through human echolocation, *Psychological Science* (submitted).

**Milne, J.L.**, Kish, D., Goodale, M.A., & Thaler, L. Parahippocampal cortex is involved in material processing via echoes in blind echolocation experts. *Vision Research* (accepted pending revisions).

**Milne, J.L.**, Anello, M., Goodale, M.A., & Thaler, L. A blind human expert echolocator shows size constancy for objects perceived by echoes. *Neurocase*, doi:10.1080/13554794.2014.922994.

**Milne, J.L.**, Goodale, M.A., & Thaler, L. Echolocation of 2D shape with and without scanning movements. *Attention, Perception & Psychophysics*, doi:10.3758/s13414-014-0695-2.

Chapman, C.S., Gallivan, J.P., Wood, D.K., **Milne, J.L.**, Ansari, D., Culham, J.C., & Goodale, M.A. Counting on the motor system: Rapid action planning reveals the format-dependent extraction of numerical quantity. *Journal of Vision*, 14(3), article 30.

Thaler, L., **Milne, J.L.**, Arnott, S.R., Kish, D., & Goodale, M.A. (2014) Neural correlates of motion processing through echolocation, source hearing and vision in blind echolocation experts and sighted echolocation novices. *Journal of Neurophysiology*, 111(1), 112-127.

Arnott, S.R., Thaler, L., **Milne, J.L.**, Kish, D., & Goodale, M.A. (2013). Shape-specific activation of occipital cortex in an early blind echolocation expert. *Neuropsychologia*, 51(5), 938-949.

**Milne, J.L.**, Chapman, C.S., Gallivan, J.P., Wood, D.K., Culham, J.C., & Goodale, M.A. (2013). Connecting the Dots: Object connectedness deceives perception but not movement planning. *Psychological Science*, 24(8), 1456-1465.

Wood, D.K., Gallivan, J.P., Chapman, C.S., **Milne, J.L.**, Culham, J.C., & Goodale, M.A. (2011). Visual salience dominates early visuomotor competition in reaching behavior. *Journal of Vision*, 11(10), 16, 1-11.

Gallivan, J.P., Chapman, C.S., Wood, D.K., **Milne, J.L.**, Ansari, D., Culham, J.C., & Goodale, M.A. (2011). One to four, but nothing more: Non-conscious parallel object individuation of objects in action planning. *Psychological Science*, 22(6), 803-811.

Chapman, C.S., Gallivan, J.P., Wood, D.K., **Milne, J.L.**, Culham, J.C., & Goodale, M.A. (2010). Short-term motor plasticity revealed in a visuomotor decision-making task. *Behavioural Brain Research*, 214(1), 130-134.

Chapman, C.S., Gallivan, J.P., Wood, D.K., **Milne, J.L.**, Culham, J.C., & Goodale, M.A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision making in a rapid reach task. *Cognition*, 116(2), 168-176.

## Conference Presentations

**Milne, J.L.\***, Thaler, L., & Goodale, M.A. A blind human expert echolocator shows size constancy for objects perceived via echoes. Oral presentation at Rovereto Workshop on Concepts, Actions, and Objects: Functional and Neural Perspectives. Rovereto, Italy, 2014.

**Milne, J.L.\***, Thaler, L., & Goodale, M.A. The perception of shape, size, and material by blind human expert echolocators. Poster presentation at Rovereto Workshop on Concepts, Actions, and Objects: Functional and Neural Perspectives. Rovereto, Italy, 2014.

Anello, M., **Milne, J.L.**, Thaler, L., & Goodale, M.A. Does a blind human expert echolocator show size constancy? Poster presentation at Canada-Israel Symposium on Brain Plasticity, Learning, and Education. London, Canada, 2013.

**Milne, J.L.\***, Anello, M., Thaler, L., & Goodale, M.A. Does a blind human expert echolocator show size constancy? Poster presentation at annual Canadian Association for Neuroscience meeting. Toronto, Canada, 2013.

Wood, D.K., Chapman, C.S., Gallivan, J.P., **Milne, J.L.**, & Goodale, M.A. Characterizing the arrival of task-relevance: Parametric delays in a rapid reaching task reveal the transition from salience-based to task-based performance. Poster presentation at annual Canadian Association for Neuroscience meeting. Toronto, Canada, 2013.

**Milne, J.L.\***, Goodale, M.A., & Thaler, L. Is there a 'retinotopic' representation of echo locations in the calcarine cortex of the blind brain? Poster presentation at annual Vision Sciences Society meeting. Naples, FL, USA, 2013.

Wood, D.K., Chapman, C.S., Gallivan, J.P., **Milne, J.L.**, Culham, J.C., & Goodale, M.A. A reaching task reveals the rapid extraction of probability information from arbitrary colour cues. Poster presentation at annual European Conference on Visual Perception. Alghero, Italy, 2012.

**Milne, J.L.\***, Goodale, M.A., Arnott, S.R., Kish, D., & Thaler, L. Parahippocampal cortex is involved in material processing through echolocation in blind echolocation experts. Poster presentation at annual Vision Sciences Society meeting. Naples, FL, USA, 2012.

Arnott, S.R., Thaler, L., **Milne, J.L.**, Kish, D., & Goodale, M.A. Functional imaging of shape processing in a blind echolocation expert. Poster presentation at annual Vision Sciences Society meeting. Naples, FL, USA, 2012.

**Milne, J.L.\***, Arnott, S.R., Thaler, L., & Goodale, M.A. Natural human echolocation in the blind. Oral presentation at annual Canadian Institute for the Blind meeting. Toronto, Canada, 2011.

**Milne, J.L.\***, Chapman, C.S., Gallivan, J.P., Wood, D.K., Culham, J.C., & Goodale, M.A. Object connectedness influences perceptual comparisons but not the planning or control of rapid reaches to multiple goals. Oral presentation at annual Canadian Physiological Society meeting. Quebec, Canada, 2011.

Wood, D.K., Chapman, C.S., Gallivan, J.P., **Milne, J.L.**, Culham, J.C., & Goodale, M.A. Visual salience of potential targets overrides spatial probabilities in a rapid reaching task. Poster presentation at annual Society for Neuroscience meeting. San Diego, CA, USA, 2010.

Chapman, C.S., Gallivan, J.P., Wood, D.K., **Milne, J.L.**, Culham, J.C., Ansari, D., & Goodale, M.A. Rapid reaching task 'points' toward different representations of number. Poster presentation at annual Society for Neuroscience meeting. San Diego, CA, USA, 2010.

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**Milne, J.L.\***, Chapman, C.S., Gallivan, J.P., Wood, D.K., Culham, J.C., & Goodale, M.A. Perception vs. action: Does the underestimation effect persist in a rapid reaching task? Oral presentation at annual Group on Action and Perception (GAP)/Canadian Action and Perception Network (CAPnet) meeting. Ingersoll, Canada, 2009.

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