Human echolocation: How the blind and visually impaired can “see” with their ears

N.A. Koning[1], M. van Doorn[2], prof. H.C. Dijkerman[1]
[1] Neuroscience&Cognition, Helmholtz Institute,
Utrecht University, The Netherlands
[2] Bartiméus, Dutch Institute for the blind and visually
impaired, The Netherlands
Correspondence to: N.A.Koning@students.uu.nl

Table of contents

(Laymen) Abstract

Echolocation is the ability to locate the objects and creatures around you by means of interpreting the reflected echoes, of sounds that bounce off of them. Human echolocation is a technique useable by any human, but most notably by the blind and visually impaired. The technique is similar to echolocation used by bats and dolphins, which use it to navigate in total darkness and under water.

There are two different forms of echolocation: active and passive. Actively producing sounds in order to receive localization information from the reflected echoes, is known as active echolocation. Passive echolocation is the interpretation of reflected echoes from sounds produced by your surroundings. Most blind and visually impaired already use some of the aspects of passive echolocation unconsciously. Active echolocation however, needs to be taught, just like the use of a cane. A trained echolocator can use echolocation to navigate his surroundings far beyond the reach of his cane and identify objects and people as if sighted.

The use of this technique requires sensitivity and rapid analysis of the properties of both self-generated sounds and its echoes, as well as the sounds and echoes produced by the surroundings. The possibilities and impossibilities, together with the known teaching methods of human echolocation are described and reviewed in detail, to better understand the influence recent research might have on teaching the technique.

FMRI analysis shows that trained echolocators, when presented with pre-recorded self-generated sounds and their echoes, have increased activation in brain areas associated with visual processing, most notably in the primary visual cortex (or calcarine cortex), as if they create a mental image.
The accuracy, detection limits and abilities to identify objects with human echolocation have also been investigated and studies on these subjects will be reviewed here as well. Research in echolocating animals is also of considerable value in understanding the possibilities of the technique and the neural pathways involved.
These and other recent research findings influence the way blind and visually impaired people are taught to use human echolocation and combine the technique with other tools.

What is human echolocation?

Echolocation is the ability to locate the objects and creatures around you by means of interpreting the reflected echoes, of sounds that bounce off of them.
There are two different forms of echolocation: active and passive. Actively producing sounds in order to receive localization information from the reflected echoes, is known as active echolocation. Passive echolocation is the interpretation of reflected echoes from sounds produced by your surroundings (Johnson, 2012).

Our knowledge of the existence of echolocation was first established in the mammals which became so well known for this ability: bats.
Bats were long thought to be able to navigate through the darkness of the night and inside caves utilizing a strong form of night vision. Their preference for the night and dark caves has seen bats playing roles in many stories and myths of different religions as well. These stories gave interesting explanations for the bat's abilities, habits and choice of residence. However, experiments spanning over the course of 1.5 century were needed to uncover the full principle of echolocation.
About 220 years ago, in the year 1793, Lazzaro Spallanzani performed experiments on bats. He covered their eyes and found they were still very much capable of navigating themselves and locating objects and prey in their surroundings, also in total darkness. He was shunned for the conclusions he drew from his experiments 6 years later, in which he stated that impeding the hearing capabilities of bats would severely handicap bats, as opposed to the covering of eyes being of almost no consequence to them. Because of the human incapability to detect ultrasound, bats were thought to be mute, thus Spallanzani's ideas seemed to make no sense. When technology permitted us to detect ultrasound, the phenomenon of actively emitting sounds and analyzing the echoes from objects in the path of the sound beam was finally recognized for what it was: echolocation (Airas, 2003).

Roughly at the same time as we came to understand the principles of echolocation, in the 1940's, the first conclusive observations and experiments on the auditory perceptual skills of blind people were performed. Before that, human echolocation underwent a similar process to bat echolocation.
It too, was not recognized for what it was at first. Rather, observers and users alike thought of it as detection of objects and the surroundings through shifting pressures in the air and other tactile input on the visage, or 'facial vision'. The concept of facial vision has been around for quite a long time and was the predominant theory. The main reason for this was that the blind people themselves said they had the sensation of object detection through the skin on their face (Griffin, 1986; Hayes, 1935).
Because of these stated sensations by the blind themselves, science tried to explain this feeling for a long time with theories on systems which were still poorly understood at that time and difficult to perform experiments on (Kish, 2003).
Some even went a step further, into more mystical explanations to explain this sensation, which was shown to be a miss-interpretation by the subjects themselves in a series of experiments by Dallenbach and his colleagues in the 1940's (Cotzin, 1942; Supa, Cotzin & Dallenbach, 1944; Worchel & Dallenbach, 1947).
Dallenbach *et al.* performed 3 sets of experiments in which 3 groups of subjects were tested: blind, deaf-blind and sighted. All participants were blindfolded. They also created 3 conditions: no additional obstructions, face covered with cloth and, lastly, hearing occlusion. In all these situations, the subjects were asked to locate an obstacle (a Masonite panel of 0.25x48x58 inches) in a test chamber (18x61 foot), with varying starting positions for both the subjects and the panel. Every subject underwent a series of trials, while indicating when they first perceived the obstacle. Subsequently, they proceeded to locate the panel only to stop as close as they thought they could get to it without getting in contact with it. Control trials were implemented where there was no panel present in the test chamber.

In trials where the auditory input was not prevented, the subjects were able to localize the panel successfully, although the blind were considerably better at it than sighted people, in terms of distance of first perception and how close they could get to the panel without touching it. This was even the case, when the researchers tried to make it more difficult for the subjects, by muffling their footsteps, or placing them in another room with headphones, listening to the sounds of a researcher with a microphone moving through the test chamber (Cotzin & Dallenbach, 1950). In contrast, hearing occlusion led to collisions with the panel in all the trials, similar to what was happening in all trials of the deaf-blind subjects. All subjects also gave no inclination at any moment during the trial that they first perceived the panel. Thus the results were very conclusive in the debate on the existence of facial vision.

Having established in their experiments that auditory input was the main sensory input and not tactile input via the face, Dallenbach and colleagues then went on to perform more experiments on the properties of sounds and echoes and the way they were perceived by the subjects. This will be described in more detail in parts 4 and 5.

Some researchers, including Dallenbach and his colleagues, then went on to try and explain why the scientific world and, more importantly, the blind subjects themselves, were led to believe that they perceived tactile input of facial vision instead of recognizing it as auditory input of human echolocation, which it actually was. These different research groups came up with various explanations.

Firstly, tension in the facial muscles and skin could be caused by fear of collision of the face with an object that is close. Thus, although the blind person perceives the object close to him via echolocation, this input is overruled by the signaling of anxiety from the facial area, making it seem like the input came from there, instead of the ears. Interestingly, even in experiments where there were no physical objects, but only the generated sounds or echoes of nearby objects played through headphones, subjects perceived tactile input.

Another explanation could have been a misinterpretation of visual input as described in another group's research. When comparing sighted subjects and blind subjects, the sighted subjects mentioned tactile input on their faces when a dim light was aimed at closed eyelids. In general the sighted subjects more often thought they were experiencing tactile input in the face when objects were near. Thus people who became blind later in their lives and have a conscious memory of visual input could have a similar tactile input on the face when perceiving nearby objects through hearing (Ono, Fay & Tarbell, 1986).

This dual sensation of tactile input combined with visual input could be caused by a special category of neurons, multisensory neurons. These neurons are associated with a system called peripersonal space and respond to both visual and tactile information (Rizzolatti, 1981; Graziano & Cooke 2006). Additionally, they respond to objects registered by the visual field as coming close to the associated body part, such as the face, possibly generating a tactile sensation before the skin of the face is actually touched. Visuo-tactile multisensory neurons are best described and the most numerous, but other combinations are also possible, for instance audio-tactile as would be the case with echolocation (Guipponi et al., 2013). Thus the fact that subjects hear an object close to their face could lead to them describing it as a tactile sensation as well (Brozzoli et al, 2012).

In contrast, Dallenbach and colleagues found no signs of facial vision at all during their experiments with 20 blindfolded sighted subjects, who were all able to identify the auditory input for what it was (Ammons, Worchel & Dallenbach, 1953).

The main conclusion of all this research was the recognition of the auditory basis of human echolocation and the link with echolocation abilities in animals as a similar mechanism.

However, the common view on echoes by the general populace is still, until this day, not geared towards the importance of reflections. Sensitivity to sounds and echoes is mostly associated with someone shouting "Echo" in an old town well, or thought to be abilities like "super hearing" of Superman or Daredevil (a blind superhero) movies. However, most of what we hear and especially most of what we see are reflections. Reflections of light on objects are processed by our eyes into an image of our surroundings with extraordinary detail. Photons (light packages that form light waves) and phonons (sound waves) are very similar in that way. Calling echoes only the echo from the well would be like saying we only perceive light "when it reflects from mirrors or highly polished surfaces" as Kish (2003) so blatantly stated it in his review ten years ago. Wherever there are sound waves, we are able to perceive their echoes, as long as they are within our hearing spectrum (Kish, 2003).

In this thesis the most recent developments in research on human echolocation of the past two decades shall be reviewed and their impact on teaching methods for the blind and visually impaired shall be discussed.

The Possibilities and impossibilities of human echolocation

According to Daniël Kish, world's first blind mobility instructor and one of the best echolocators, human echolocation gives the blind and visually impaired more possibilities to perceive and navigate their surroundings and thus a means of self-reliance. It can be a powerful tool, but it is not without its flaws. Therefore, it is often taught to be used in conjunction with other tools for the blind, like the well-known, white cane (or long cane) or guide dogs.
Just like with most tools, human echolocation requires quite extensive training. Although you are born with the means, other and especially visual information is often dominant. With echolocation, you need to be especially aware of the sounds, to perceive the echoes and interpret them.

Most blind people (both from an early age and people who became blind later during life) are familiar with some of the aspects of passive echolocation, since hearing is a more important source of information for them than for sighted people. However, almost none are (initially) aware that a part of what they hear is actually echolocation, until they are taught in the technique. With active echolocation this goes even a step further. Here the user is consciously producing a sound and interpreting the echoes, which requires training in the use of the correct types of sounds in different situations and additional training in echo interpretation. Also, the technique requires the user to learn to integrate the newly gained information with the input of the other senses. Context is very important for the interpretation of the echoes and sounds.

This is illustrated by Gagnon *et al.* (2010), whom experimented with restrictions on environmental cues involving navigation. They made various tactile multiple T-mazes, sized to navigate with your index finger, with 12, 16 or 20 decision points where a participant needs to decide where to move the finger towards next. They compared congenitally blind (CBs) individuals with sighted controls (SCs) who were blindfolded, by measuring the number of errors made while negotiating their way through the maze during several trials. The small scale (finger-size, instead of man-size) of the mazes greatly impairs environmental cues, used in echolocation. It is these environmental cues that CBs are used to and rely on when navigating their way through their surroundings in daily life. They show that the SCs perform better in these tasks, consistently making fewer errors than the CB participants. There are no direct apparent differences between the groups that would make it easier for SCs to navigate the mazes than for CBs, since the main, most obvious difference, blindness, has been mitigated by the blindfold. Therefore, the main explanation for this difference is context. In the small scale of the mazes, the effects of proprioceptive input and echolocation are less effective or even unusable for these fine movements in the confined space required to navigate them. Instead, they have to rely solely on haptic information from their index-finger navigating the maze. Gagnon et al. (2010) argued that the way people structure their surroundings (their perspective) according to the information they receive from their senses is thought to play an important role here. They argue that CB participants utilize a route (also called egocentric) perspective, as if you are standing in the maze yourself and walking the route through the maze. The SCs on the other hand, use a survey (also called allocentric) perspective, as if looking top down onto a map of the maze, which would make it easier for them to make fewer errors. This survey perspective is particularly linked to visual perception.

In addition to context, this experiment also indicates the importance of size. The smaller and finer the objects are, the more difficult it is to acquire a concept using echolocation, both passive (less ambient sounds reflecting of the small parts giving specific information) and active (many active generated sounds are required very closely to acquire a bit more detailed information)(Stroffregen et al., 1995).

However, in situations on a larger scale, where environmental cues are more important again, the blind can have the advantage. Our vision, for example, however accurate, enabling us to sweep over an area very quickly, does not allow for us to see behind us simultaneously, as we do not have eyes in the back of our heads. Echolocation does not have this restriction, as we can perceive sounds and echoes all around us. Just like greater detail of vision is acquired binocularly, acute awareness and interpretation of sounds and echoes is only possible binaurally. That allows us to pin-point information like location relative to us, as well as distance (in the case of echoes) (Gagnon et al., 2010). Stoffregen and Pittenger (1995) already pointed out that “certain informative relations are fundamentally unavailable to a single ear” and thus “the two ears must be considered as parts of a single perceptual system” (Stroffregen et al., 1995).

One of the great assets for the blind echolocator over normal cane use is that more information can be gained in a short period of time by exploring the surroundings with active echolocation. When entering an unfamiliar room, a sighted person usually stands at the door and sweeps the area with his eyes, taking in the overview of the room. A blind cane user would have to walk around the room to get this same overview via tactile interaction with all the objects in the room. An echolocator can do the same as a sighted person, although it takes a bit more time, by generating sounds (usually tongue clicks, but more detail on this in chapter 3) and interpreting the echoes. Echolocation is also called “Flash sonar” for this very reason, because it is similar to exploring the room in complete darkness by flashing a flashlight on and off. Experienced echolocators only need a few “flashes” to scan the room, so even while it is not as fast as actual sight, it is definitely an asset. As Aquanetta Gordon, the mother of Ben Underwood, a young blind kid and natural echolocator, pointed out to her son when he said “Mom.., man, I wish that I could see”: “Ben, but look what you can do. If we had a blackout right now, everyone would have to follow you!”

It is clear that echolocation can give the blind users a lot of freedom of mobility. It allows for navigation and avoiding collisions, even from moving objects, like other people, bicycles and cars.

Experienced echolocators like Daniël Kish and Ben Underwood can even be seen cycling or rollerblading through their neighborhood. The fact that they can do this means that the information gained from echolocation encompasses movement and velocity assessment.

Vision gives us (almost) constant feedback about our actions (excluding factors such as blinking), while echolocation has a delay between sound generation and echo perception, limiting the speed at which we can generate sounds and interpret them.

Lee *et al.* (1992) studied this in bats and showed that one generated sound and its echo already contain the necessary information, instead of having to compare the input of 2 consecutive sounds and their echoes. They introduce the ‟ταυ-function”. This function was derived from the retinal tau concept, which was first introduced by Lee in research on what information is available to the visual system (on the retina) while moving (Lee et al., 1976). In this research Lee establishes that ταυ is a relative variable; independent of how the eye is moving, because the movement generates an optic flow field (you are in motion, so the perceived environment is in motion as well). Lee and his colleagues argue that the same principle can be applied to the auditory system and call it an acoustic flow field. This ταυ-function is an estimate of time-to-contact with any given object detected in the acoustic flow field at a certain distance, being approached with a certain velocity. From this function it is possible to derive the acceleration/deceleration in the equation needed to avoid collision. As a bat emits a sound, it bounces off of different parts from the same surface of the object, which can be detected in various ways:

1) The angle at which the different echoes approach the head,
2) The timespan between the emitted sound start and the echo start from the different parts of the object,
3) The difference in intensity of the echoes, based on the fact that you know the intensity of the originally emitted sound.

As Lee *et al.* point out, these three methods can all be perceived monaurally, thus if both ears receive this auditory input, even more detailed information on movement in our surroundings is possible. They describe this as an ambient auditory flow field, similar to the flow field of vision as used by birds and humans, but acquired through echolocation and all around you in 360° (Lee et al., 1992). This research shows the several possibilities of human echolocation in navigation and localization.

Object recognition, on the other hand, is often more difficult. The echolocator must either use his other senses to gain more information about the object, or already be familiar with the type of object and hear specific characteristics of the object's echoes in order to recognize it. If the echolocator is familiar with the object, it is possible to recognize nuances in the echo revealing more details about the shape of the object and the materials it is made off. But this requires experience and familiarity with the materials sound reflection and the object, both through training and previous encounters with similar objects. The echolocator must be familiar with the unique timbre of the object's echo; the combination of frequencies generated by the reflection of the self-generated sound (Kish, 2003; Johnson, 2012). Interpretation of the timbre of the object's echo is only possibly through training, to become familiar with the self-generated sound used for active echolocation and the properties of the echo it creates.

To summarize, it is possible to train and learn how to use human echolocation to detect and navigate one's surroundings from a distance with a general, 360° all-around view, while Flash sonar allows for more detail when needed. Due to the concept of $\tau\alpha\upsilon$ not only static objects, but also movement is detectable. High detail and object recognition are harder to perform with human echolocation and require a greater level of skill, training and experience with identification of different shapes and materials.

In order to understand the full extent of these possibilities and impossibilities of human echolocation described above, it is important to consider the alternatives.
The earliest and most well-known aid for the blind and visually impaired is the cane. The cane is effectively a tactile extension of the arm and hand. The principle is similar to echolocation as it is also possible to speak of passive and active touch. Just like passive echolocation gives less information than active echolocation, so does being touched by someone or something give less information than actively touching the object or person yourself; i.e. we learn more from self-generated and resistive forces than "incoming" forces (Stroffregen et al., 1995). The important difference here is reach. With echolocation experienced users have been shown to detect objects from meters away, further away than a cane can reach. However, the smaller and closer to the ground objects are, the more difficult echolocation becomes as described earlier, while a cane is better suited to detect (smaller) obstacles on (or close to) the ground, when used in the typical sweeping motions in front of the cane user. The complementary roles for human echolocation and cane use will be described further in chapter 3 of this review and onward.

Another category of "aids", in development for a much shorter time than the cane, is the category of sensory substitution devices (SSDs). In conjunction with that category are sensory enhancers, a broad category ranging from cameras (used in SSDs or in infrared and night vision goggles) to glasses and hearing devices, which are in common use, or even adaptive sensory enhancers such as sonar in submarines allowing us to listen under water. SSDs are devices used to translate one form of sensory input, detected by the device, into another form of sensory input which can be perceived by its user. The most notable variants include visual-audio sensory substitution (VASS) and visual-tactile sensory substitution (VTSS). VTSS devices utilize a grid placed on sensitive skin on which tactile stimuli are projected based on what the device sees with its camera. Test results show that with a short period of training (5-15 hours) with the VTSS device, it can be used quite effectively with blind subjects even discriminating between different people, their general attire and the movements they are making (Ward et al., 2009). However, the VTSS grid is relatively impractical in daily use as it is a highly powered device, thus not very easy to take with you. In contrast, VASS devices are much easier in that regard, as they use simpler means of conveying the sounds; i.e. via regular headphones. The camera's visual detection is translated into certain sound patterns (increase in frequency from bottom to top, together with horizontal scanning in time or increased frequency from left to right) and then send to the users ears (Auvray et al., 2007). No comparison between these devices and human echolocation has been performed till date, but some of the results of separate studies to the different methods can be compared. The recognition of objects is possibly easier with a VASS or VTSS than with human echolocation, however it still feels as if someone is sketching the world in rough outlines in black and white. Additionally, recognition time is often between 0.5-1 minute. Thus it would be more difficult to traverse traffic using a SSD than with human echolocation (and a cane), which gives almost immediate feedback. Participants in SSD studies encountered difficulties when large camera movements were made to track a target object. They often lost the object and had difficulty relocating it as well. Thus the responsiveness of human echolocation seems evidently better than that of SSDs. Sensory enhancing echo-locating devices, based on the same principles as sonar, like submarines, emit ultrasound and/or FM signals and interpret the echo. This interpretation is then translated into sounds that are audible for humans and relayed via headphones to the user. The information gained from these echo-location SSDs is similar to what human echolocation can provide the user with (Auvray et al., 2007), but with less detail and less direct than when the sound is self-generated and interpreted directly.

Even though the use of technology for aiding visually impaired individuals is not yet as advanced as human echolocation, it is not unthinkable that, like a cane, SSDs can be valuable additional tools. Especially when the technology allows for adaptation to certain situations our natural senses are not capable off. Sonar, as mentioned above, is used by submarines to navigate underwater. It should be possible to use the knowledge from current research on dolphin underwater echolocation and the unique adaptations in these animals for that purpose (specifically the dolphin's ears for reception of the self-generated sounds underwater) in those devices. Thus it would be possible for experienced echolocators to swim using echolocation, or even go scuba diving and "see" underwater like the dolphins (Hemila et al., 2010).

It has become clear that human echolocation has several advantages, over conventional "aids" and even in certain cases compared to sight. It's reach is far beyond the tactile range of a long cane and flash sonar clicks are quicker and cover a larger area instantaneous compared to moving a cane around or reaching out with one's hands. Navigation and crossing difficult terrain, or even swimming (underwater), can be new possibilities a blind individual did not have without the technique. As of yet, human echolocation is also still more effective than most artificially manufactured aids.
However, it can be difficult or impossible to detect features of very diffracting or less solid surfaces, or anything else that dampens the echo, such as respectively the ground closely in front of the user or a chicken wire fence. Additionally, it requires familiarization with the self-generated sounds and their echoes, involving much training to master the technique and even then it remains difficult to reach a great level of detail and recognize objects without additional information from other senses.

Both the advantages and disadvantages or possibilities and impossibilities of human echolocation are largely based on the properties of the echoes, which will be reviewed further in chapter 3.

Analysis of echo properties

An echo has many different properties, which all contain information and distinguish echoes from each other. This became apparent in chapter 2, because learning to interpret these complex echoes requires training and different exercises to recognize the intricacies of an echo. Therefore the properties of echoes, from both human echolocators and other mammals, will be analyzed further here and consecutively in chapter 5 the perception and neural processing of echoes and their origin sounds will be studied.

Each sound and its echo have several categories of properties (Johnson, 2012; Kish, 2003):

1. Frequency and pitch
2. Volume or loudness
3. Phase of overlapping sound waves
4. Timbre
5. Pulse-echo-delay

1.) The frequency of a sound is inversely linked to the wavelength of the sound. Hence a low frequency sound emitted by an echolocator has a long wavelength and thus a longer reach before it dies out. This is useful if the echolocator wants to "look" further ahead. A higher frequency has a shorter wavelength, thus decreasing its range, but increasing its density and energy, which reflects better off of objects back towards the sender. A high frequency, short wavelength sound wave is therefore more useful in detection of more difficult (and most notably smaller) objects (Kish&Bleier 1994-2000). Davies and colleagues (2010) also show that the accuracy of high frequencies is better, using an ultrasound emitting and translating device (AUDEO, Audification of Ultrasound for detection), which translates the echo of the ultrasound pulse to an audible tone. The detail of distance determination and direction within a relatively confined space of a 5x5m anechoic test chamber is higher than normal human echolocation. In general however, long distance or detailed information is not needed for everyday navigational purposes, thus a self-generated sound with a wide midrange frequency would be sufficient and give the most information from a broad echo spectrum at the same time.
Humans perceive frequency as pitch; the steps in which the auditory system is able to discriminate between frequencies. Most human senses are less effective at absolute discrimination (in this case an exact frequency) and better at comparing between two or more different inputs. Pitch allows us to perceive the differences between high or low sounds to a high level of detail, with up to 1400 different pitches within the range of our hearing (Johnson, 2012). Kish & Bleier also touch on this subject when they give advice on designing training exercises for students of human echolocation, stating: "It is much easier to compare two different echo qualities when presented together than at different times" (Kish&Bleier, 1994-2000).

2.) The volume (or loudness or intensity) of the self-generated sound is directly tied to the intensity of the rebounding echo. A louder sound facilitates a longer travel path for the sound and its echo, enabling object detection over greater distances. However, the sound cannot be dragged on longer to achieve greater intensity, because it would hamper echo detection and recognition. Additionally, if the sound is too loud itself, it can block the sound of the returning echo, because the sound has in most instances not died out yet when the echo returns. Thus if the original sound is too loud, it can mask the echo completely. A balance between sound and echo intensity must be acquired for effective use of echolocation(Stroffregen et al., 1995; Kish, 2003).

3.) The phase of sounds is determined by its frequency, the speed at which the sound oscillates. Two of the same sounds have the same frequency, but not necessarily the same phase as well. If the sounds have the same phase, when they interfere with each other, they enhance each other and the sound gets greater amplitude, thus becoming louder. The opposite can of course happen as well, when they are out of phase, the oscillations can diminish the total amplitude, or even extinguish the sound entirely. As described in chapter 4, different self-generated sounds can be more helpful in different situations. When the ambient noise consists of more high or low frequencies, it is useful to choose a sound in the opposite range of frequencies, to prevent extinction by overlapping sound waves coming from the surroundings (Johnson, 2012).

4.) Timbre is especially important for sound and object recognition. The timbre is the unique intermingling of frequencies from a sound to form a unique wave pattern which can change over time (something a single frequency cannot do). For this reason it is also referred to as tone color. In a timbre it is possible for one frequency to die out or a new one to add to the existing set of frequencies, thus changing the tone's wave pattern. As long as a human echolocator has encountered such a unique sound before, it is possible to identify the identity of the object, material or person, with the combined use of passive and active echolocation (Johnson, 2012).

5.) The pulse-echo-delay, the difference between the moments the pulse sound directly reaches the ears and the moment the echo reaches the ears, relays information about two factors important for navigation: distance and direction. Distance can be determined as the time difference of the pulse-echo-delay for the speed of sound, divided by 2, because the reflection travels back over the same distance as the origin sound. As described earlier, pulse-echo-delay can still be perceived monaurally, however, to establish the direction at the same time as well requires the same information to be received binaurally, to subsequently be processed in the brain from both sides (see also chapter 5) (Stroffregen et al., 1995; Takahashi et al., 2008; Devore et al., 2009). Takahashi and colleagues describe that in barn owls, similar to human vision, there is a representation of a three-dimensional space map in the auditory part of their brain in the external nucleus of the inferior colliculus, which allows them to hunt at night as well, although they do not echolocate actively, only passively. Just like in visual and tactile systems, the neurons in this area use the spatial acuity system to identify the locations of two different sound sources with overlapping receptive fields (RF's), giving information about the level and difference in arrival-time between the ears. The authors suggest that the same neurons are also able to determine "what" the owl is hearing, in addition to "where" the sound came from, at the same time. "Where" is determined by which neurons are activated on the topological space map in the auditory cortex, while "what" is conveyed by the firing rate and pattern of these neurons, corresponding to the sound's or the echo's properties (frequency, volume and timbre) (Takahashi et al., 2008). Of course the latter requires previously acquired knowledge of the "what", for a certain material, object or even person to be recognizable.

A trained human echolocator can use the first two factors, pitch and loudness, to echolocate with greater detail and over greater distances. Schenkman & Nillson (2011) compared these two important factors in an attempt to determine the overall impact on human echolocation. As pitch and loudness co-vary when sounds are generated, this comparison could not be studied earlier, but now the authors have manipulated sound recordings, made in a real environment, as to vary either factor artificially while keeping everything else as constant as possible.

The recordings were made in an office via an artificial head to mimic the normal situation as much as possible and via a cable an object could be moved through the room at various distances (100, 200 or 300 cm) from the head. Then the recordings were manipulated to contain pitch or loudness only, replacing the other factor with the information from the recordings containing no object. The original recordings were used to test the pitch + loudness condition. Thus each blind participant underwent 9 sessions for all combinations of the 3 different conditions and the 3 different distances, with 56 trials for each session. The recordings were played with earphones.

This experiment showed that at 100 cm distance, for all 3 conditions the accuracy approached 100%. At 300cm distance, performance dropped strongly, approaching chance level for all conditions, but a clear and significant distinction became apparent at 200 cm distance. Pitch and loudness together gave the highest accuracy, as expected, but closely followed by the pitch only condition, while the loudness condition was less accurate. This indicates that Pitch is the most substantial contributor to effective human echolocation over loudness. To further investigate this, the same 3 conditions were also presented to sighted participants at distance 200 cm. Again the pitch + loudness condition was the most accurate, followed by the pitch only and lastly the loudness only, however, the first 2 conditions were significantly less effective in the sighted participants compared to the blind participants. The loudness only condition was not significantly different between the sighted and the blind, which would indicate that the training of echolocation skills is mostly reliant on improving pitch detection and interpretation (Schenkman et al., 2010; Schenkman&Nilsson, 2011).

The loss of accuracy at 300 cm distance to values approaching chance level is not as sudden or strange as it might seem. Devore and colleagues (2009) showed that reverberation (echoes reflecting on multiple surfaces over time) degrades directional sensitivity. The longer a distance the sounds and echoes have to travel, the less effective a human echolocator (or listener in general) can estimate source position (Devore et al., 2009). How much interference is generated by reverberation and increasing distance in active echolocation is also dependent on the self-generated sound used. Different sounds have different frequency sound wave spectra, thus making them more or less effective. Of course the size of the object is also important, the test object used by Schenkman & Niilsson (2011) was of a size reasonably detectable at 100 or 200 cm (an aluminium sheet, diameter 0.5m, 1.5mm thick), but too small for 300 cm. A larger object would be detectable from further away, but again the distance at which it is detectable will differ based on the factors studied by Devore et al. (2009). Rojas and colleagues (2008) chose natural generated sounds over artificial sounds, because these natural sounds carry your own individual acoustic signature, to which our auditory system is more attuned and because the user is independent of any technology and possible failure of the devices. As described in point 1, a broader frequency spectrum allows for more detailed information and a shorter self-generated sound (points 1 and 3) is less likely to interfere with its echo, thus giving more information. Rojas et al. found that the palatal click exceeds the other tested natural sounds in both these aspects (Rojas et al., 2009).
However, Johnson (2012) took this one step further and compares more self-generated sounds (both natural and artificial) by means of their frequency spectra, showing that multiple candidates are likely to yield good results when used in echolocation. One general aspect he indicates is that the human auditory system is more sensitive for frequencies around 3 kHz, detecting sounds with a lower intensity in this area of the auditory spectrum (Johnson, 2012).

In general, it can be concluded that all these 5 categories of different echo properties are important for the use of human echolocation and are predominant in their own certain situations when an echolocator navigates his way through his surroundings, adding to range or accuracy, detail or echolocating speed. However, the first 2 categories, frequency/pitch and volume/loudness, can be considered the most important in overall use. Frequency/pitch makes it possible to acquire greater detail or a more general overview, depending on the frequency used and is the most important factor in the feedback loop from a dynamic environment, as a higher frequency can tell you more about the changing surroundings. Volume/loudness variation is important for reach and distance determination and can contain information about complexity and object material as well. Reach is one of the major advantages of the human echolocation skill over other, more conventional aids for the blind like the white cane and object identification is the other, since these are important for environment navigation, its primary everyday use.

Unfortunately, although we are born with the means to echolocate, we still have to learn how to interpret the echo properties described above before we can actually use the technique. Thus chapter 4 will review the known teaching methods of human echolocation till date.

Known teaching methods for human echolocation

Currently, there is no single teaching method for human echolocation, where you follow a certain set of steps which will guarantee that at the end, the student has mastered the technique. Instead, there are various principles or guidelines describing the different aspects of human echolocation students need to learn. Depending on different factors, some students may already have mastered aspects important for echolocation by themselves, or require more attention to one aspect and less to other aspects, which come easy to them. This is similar to teaching in school, where different methods of explanation and different exercises are effective for different students, depending on factors such as development of spatial awareness (especially in early blind people), age, personality, parental views on upbringing, gender and development of the body and mind (Johnson 2012; Kish&Bleier, 1994-2000; Kish, 2003).

Possibly the most important aspect to realize when teaching echolocation, is that the student needs to relearn how to interpret auditory information. To recognize sounds and echoes in the environment and distinguish them from each other requires training and exercise, tailored to the person who's being taught. When the student is aware of this, passive echolocation skills are starting to develop. However, as Kish & Bleier (1994-2000) describe it, passive echolocation alone is still limited. If you only use passive echolocation, "it would be like a hiker with no flashlight trying to see a treacherous mountain path at midnight by the light of other, scattered hikers' flashlights. You might see something and what you see might even be recognizable to you, but you would not be able to walk safely along the path" (page 10, Kish&Bleier, 1994-2000). To be able to safely traverse this path, you need your own flashlight, your own Flash sonar: active echolocation.

Active echolocation involves learning to generate one or more sounds yourself and detect and interpret the echoes from these self-generated sounds. There are many different self-generated sounds possible. Tapping the white cane, snapping your fingers, clapping your hands, the ring of your keys, clicking with your tongue, a handheld clicker or your own footsteps. Each has advantages and disadvantages and it varies between individuals what a student feels most comfortable with. It is therefore important to try out all different possibilities when teaching human echolocation to someone. There is a certain emphasis on the tongue click, because a few of the world's expert echolocators utilize it and it is what most resembles the chirps bats make (Kish&Bleier, 1994-2000; Johnson, 2012; workshop Bartiméus on human echolocation, 15-1-2013, Zeist).
Advantages are that echoes tend to return to the point where the original sound came from and with the tongue click this would be your head. Also, because it is formed by your mouth, it is a directed sound into a cone in front of you, which makes it easier to interpret the auditory information one gains from it and allows for directed investigation of an object more easily (Kish&Bleier, 1994-2000; Johnson, 2012). However, it is not possible to click and talk at the same time for example and the click has a relatively weaker maximum of loudness that can be generated, compared to clapping your hands, which limits the range of detection. Clapping your hands cannot only be much louder, it also generates a sound in all directions (except where it is blocked by your own body), but requires 2 empty hands to use, which is not always practical. A handheld clicker only requires 1 hand, but takes more time to get used to the sound and its echoes than a tongue click or hand clap, because these sounds are already familiar and can be difficult to use in certain places, where the surroundings are crowded. Tapping the white cane can be very useful as you can tap on the surface you walk on, but can be muffled by a soft underground and lessen the amount of tactile information gained from it. Also, as the tap originates further from the head (than a tongue click, hand clap, hand held clicker or keys) the echo returns further from the head and nearer to the cane, feet and the ground, losing information (Kish&Bleier, 1994-2000). The ring of keys is closer to the head, held in one hand and the various keys generate a broad sound spectrum in all directions (similar to a hand clap), potentially

returning more information in the echo. At the same time the jingle of the keys can be confusing and more information in one echo can also make it harder to distinguish what is what.

The properties of the different generated sounds and their echoes are essential to their utility and are therefore analyzed separately in chapter 3 and compared with studies on echolocating animal species in chapter 6 in the conclusions and discussion (chapter 7). For example, at least some of these methods allow for differentiation in the properties of the sound and its echo: someone can use different types of tongue clicks or clap louder or softer, or differ its sound through hand positioning, thus being more flexible in their use. Each sound has its own advantages and disadvantages, thus not only trying all of them out, but learning to use at least 2 different methods to complement each other in certain situations would be advisable.

For each signaling sound chosen by the student, training and exercises need to aim at learning to interpret echoes correctly. What is the position of an object relative to the echolocator? At what distance is it? The height and size of the object and where it begins and ends can be determined. Both the object and the observing echolocator can be static or dynamic and all combinations can only be learned to identify through practice. The angle at which the object is being approached is detectable by binaural differences. The shape of the object can be identified, with certain surfaces being much harder to recognize via echolocation (especially round surfaces) than others (flat surfaces). Together with information about complexity of the object, which can also be learned from the echo, especially after previous encounters with a certain material, the student can in the end learn to identify objects from a distance using echolocation, instead of having to touch it to know what it is (Kish&Bleier, 1994-2000; Johnson, 2012). All the currently available sources on teaching methods, from literature (Kish&Bleier, 1994-2000; Kish, 2003; Johnson, 2012) and practice such as workshops (workshop de Markgrave with Daniël Kish on human echolocation, 18-12-2012, Antwerpen ; workshop Bartiméus on human echolocation, 15-1-2013, Zeist), describe a similar pattern as a guideline to learn this identification process with different self-generated sounds. These guidelines are based on the properties of self-generated sounds and their echoes, as described in detail in chapter 3. Static targets are easier to detect than moving objects and the same applies to the student him- or herself standing still or moving around. Size matters as well, in general larger objects are easier to detect than smaller ones, thus for every variable (e.g. movement or distance for example) begin with larger training targets before continuing with smaller ones. This can be combined with the complexity of targets in shape, texture (hard/soft) and permeability for sound (less solidity returns less echo) before going to a smaller size. Making use of everyday environments, both in- and outside, and using objects in these environments is generally most effective and more fun for the student as well, since the student can use what is learned immediately, which stimulates practice of the technique outside of teaching sessions as well.
Additionally, this buildup of learning the skill of human echolocation familiarizes the student with its advantages and shortcomings as described in chapter 2.

Indicative of what a student can learn to do, is the study of Teng & Whitney (2011), who showed that a trained (early blind) echolocator can discriminate between 2 objects at a 1.58 degrees angle of separation in 75% of the tests and that with increasing angle the accuracy improves rapidly to nearly 100% at about the same angle where the best sighted, blindfolded test subject reaches the 75% threshold: 3.76 degrees. Although this spatial resolution is not as good as visual spatial discrimination, it is still remarkably acute and more accurate than previous research had indicated. In their experiments Teng & Whitney further showed that sighted participants can learn to echolocate reasonably well (within 4 test sessions) and improve significantly over the various sessions. They can reach similar levels of accuracy to a blind human echolocator, trained through use of the technique in daily life, albeit at closer range and with much larger angular size differences. At the same distance, sighted participants perform just above chance level (about 60% correct answers), while the blind trained echolocator already reaches accuracy levels above 80% at this distance, which is only reached by the sighted participants at half the distance and double or triple angular size differences (Teng et al., 2011).

A logical next step is integration with other navigation skills such as cane use. Although someone might have a considerable skill level in both techniques separately, combining and integrating them is often difficult. It requires the student to divide attention between echolocation and cane use, which in turn requires more training and exercises for which both skills are needed, to reach the same level of skill as when they used the techniques separately before (Kish&Bleier, 1994-2000). For effective mobility integration of different skills is paramount, as each individual technique has possibilities and impossibilities, as described previously in chapter 2. Just like different sounds can complement each other in the use of echolocation, combining echolocation with other techniques can complement for each other's shortcomings as well.

When these techniques are effectively integrated, the three main factors for blind mobility are greatly enhanced, leading to more efficient, secure and effective travel (Leonard, 1972; Armstrong, 1975; Kish&Bleier 1994-2000; Kish, 2003):

1. Negotiating objects whilst avoiding bodily contact with the objects
2. The ability to stay on a path without accidental departure
3. The ability to cross streets or other open spaces quickly, efficiently, directly and safely without incident.

Perception and processing of sensory echolocation input in the brain

Only since recent technological advances it has been possible to study the underlying mechanisms of human echolocation perception and processing in the brain.
Research of perception in blind people from the past decade indicates that the largely unused visual part of the cortex shows signs of activity when other sensory information comes in, especially when this involves visualization or imagery of the observations. For instance, the visual cortex is activated when reading braille (Burton, 2003) or when someone is dreaming (Johnson, 2012). Similar findings were observed when studying an echo-based visual-to-audio SSD (sensory substitution device), in early blind subjects. This study showed increased activation of the visual brain areas, measured using positron emission tomography (PET) (Ciselet et al, 1982; De Volder et al, 1999; Thaler et al, 2011). Thaler and colleagues (2011) followed this concept in their study to investigate if the visual cortex is also activated in addition to the auditory cortex when human echolocation is involved. The subjects in their study where presented with recorded self-generated sounds and echoes from the blind participants in 3 different conditions: 2 were in an anechoic chamber and the subjects were asked either keep the head stationary or move the head. Objects with a concave or flat surface were placed in front of them or at a 20° angle to the left or right. The 3rd condition was outside, with either a tree, car or lamp post in front of the participant. The recordings were then played to the participants via nonmagnetic headphones to allow measurement of brain activation via functional MRI (Magnetic Resonance Imaging). The BOLD (blood-oxygen-level-dependent) signal was detected as a measure of brain activation and compared between early blind (EB), late blind (LB) and control participants. Upon hearing the sounds, all subjects showed activation in the auditory cortex, although the activation in controls was more robust than in EB and LB, because EB and LB are more accustomed to the sounds and echoes. However, additionally both EB and LB exhibited increased activation in the visual cortex (calcarine sulcus and surrounding brain areas) as well. Furthermore, the increase in activation was greater for EB than LB, indicating that the early onset of the blindness allowed for greater adaptation in the brain. Most likely it is for the same reason that only EB showed a contralateral bias in the occipital lobe, where more activation is measured in the left hemisphere when the object is detected to the right and vice versa, similar to the way our eyes function. This difference was not detected in the auditory system of all participants (Thaler et al, 2011).

When EB and LB were presented with the recordings of the conditions where the head was moving, both showed increased activity in regions adjacent and inferior to the ITS/LOS junction, (visual) motion processing associated areas of the temporal lobe, while controls showed no reaction (Thaler et al, 2011). However, other condition differences related to object shape yielded no significant differences in activation, even though EB and LB were able to distinguish between them and stated to perceive them as different from each other.

It is still unclear in what manner the visual cortex of the blind is repurposed and this requires more research. Thaler et al. (2011) themselves continued to investigate participant EB’s activation in the brain with new tests as well (Arnott et al, 2013). They designed experimental conditions to record echolocation of different object features. These recordings could be played back through the earphones in an fMRI scanner as in Thaler et al (2011). The features tested were shape, location and material of the object. Four objects of different material and shape were placed at different locations around EB and the control participants (congenitally blind; CB and late blind; LB), whom were asked to echolocate in order for sound and echo to be recorded and used in the test paradigms. Just as in their study in 2011, the authors found activation in the occipital lobe, but no clear differences between the various features were found yet, with the diversity of activation patterns in the subjects on different feature tests being very high.
The variation can be found in what parts of the visual cortex are activated. In EB there seems to be a topological representation, similar to when sighted people process information from the eyes. In LB

and CB, this is not the case, thus it seems to be an adaptation that is only possible when becoming blind at a critically early age (Arnott et al, 2013).

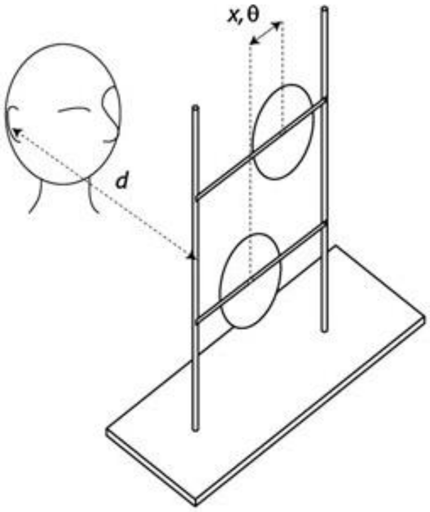
Despite the indecisive results in the Thaler et al (2011) study, it might be possible that the repurposed neurons play a role in object and shape recognition, since this is a main feature of visual perception if the eyes would still be functional. Haptic recognition of these features takes place in the same and surrounding brain areas, thus integration with information (previously) gained through touch is also possible.

Hoshino&Kuriowa (2002) describe the role of the inferior colliculus (IC) in interaural interpretation of auditory stimuli when using human echolocation. Unlike natural echolocators (such as bats), they state, humans have to interpret what they hear in most aspects. Bats have a topological map in their brain, where a certain place in the brain corresponds with a certain distance of an object, based on the echo delay (Palakal&Wong, 1999; Hoshino&Kuriowa, 2002). In humans, Hoshino&Kuriwa suggest that only 7% of IC neurons are capable of forming such a map through their sensitivity to interaural onset time differences, thus a human variant would be far less sophisticated than the bat's map. The auditory system's topographic (tonotopic) map is based on the hair positions in the cochlea, thus it is a frequency map and no distance/echo delay map. However, it might be possible that with training, this ability is strengthened by a part of the repurposed neurons from the visual cortex as found by Thaler et al (2011). The visual system utilizes a similar topological system in congruity with the retina of the eye (retinotopic map), thus the visual brain area could be capable of forming such a topological distance/echo delay map instead. Further research on the functions of the repurposed neurons is therefore necessary to better understand its new function(s).
The visual brain area is probably used by the blind echolocator to overcome limitations of the human auditory area. Humans and many other non-echolocating animals possess a mechanism of echo suppression, favoring the direct, initial sound called stapedious reflex, which is complemented by the neural refractory period (Carison-Smith&Wiener, 1996). It is a protective mechanism aimed at preventing permanent damage from very loud sounds and prevent al sounds from blurring together, increasing distinguishability from consecutive sounds (such as speech or music). This mechanism only suppresses echoes within the first 2-3 milliseconds (Kish, 2003), thus echoes from objects over longer distances do not suffer from suppression, but objects within 2-3 meters send back an echo within this timeframe and are suppressed (Schenkman&Jansson, 1986; Kish, 2003). However, the same mechanism also enhances the initial sound and an echo from further away which is not surpressed essentially returns as a new sound and as such it can profit from the enhancing effect instead. Additionally, when an echo is coming from a close object, it suffers less from reverberation along the way and is clearer to distinguish and identify in the first place while the onset dominance of this mechanism can actually be used to acquire more directional information, "resulting in more robust estimates of source position" (Devore et al, 2009).

Just like Thaler et al (2011) used audio recordings in their MRI experiment, Schörnich and colleagues (2012) went on a step further and tried to create a virtual echo-acoustic space, using live recording microphones and the generation of appropriate echoes for differently positioned virtual reflectors via headphones. These generated echoes were based on an analysis of the clicks and echoes recorded with real reflectors. The subjects generate a click, the microphone registers the click and a matching echo for a reflector at a certain angle is played via the headphones with a differing time delay, simulating different distance in addition to angle. This allowed the researchers to determine the relation between angle and distance recognition as well as the accuracy of object perception relative to each other. At lower angles the detection results are mixed, but at 45° an improved detectability of target-range was found, leading the Schörnich and colleagues (2012) to hypothesize that the second reflector functions as a temporal reference for binaural and timbre comparison, thus increasing accuracy, in opposition to the hypothesis of the comb filter effect: higher fundamental frequency from added echo strength to the direct signal would be stronger when the two reflectors

are nearer to each other, but a smaller angle leads to deteriorating performance instead of better performance. From these results the authors suggest that temporal resolution and timbre are possibly more important than pitch cues, but already state themselves that the evidence for this conclusion is only circumstantial.
This study also showed that the subjects changed their tongue clicks during the tests as they tried to reach optimal performance and the majority of subjects used “relatively loud, short, broadband tongue clicks to solve the task”, as described in chapter 3 to be very effective self-generated sounds (Schörnich et al, 2012).

At the same time, Teng et al (2012) performed a series of tests to find what level of spatial resolution expert (10.000+ hours of training and use) human echolocators can reach. To determine this, they searched for the minimal angle at which a human echolocator can discriminate which of 2 presented stimuli is more to the left and compare it to the spatial resolution of the visual system. They used an auditory adaptation of commonly used procedures that test perceptual acuity. Two lines are shown and the subject needs to determine which one of the two is higher (Figure 2). The auditory analogue task involves a two alternative-forced choice (2AFC) discrimination procedure with two disks positioned above each other (Figure 1). The subject has to determine whether the top disk is positioned towards the left or right of the bottom disk, thus auditory perception is tested over a horizontal axis (Figure 1) and not over a vertical axis (Figure 2), in order to test human echolocation’s maximum potential. Vertical tests are common, but as explained below * the spatial acuity of the auditory system is more acute horizontally than vertically.



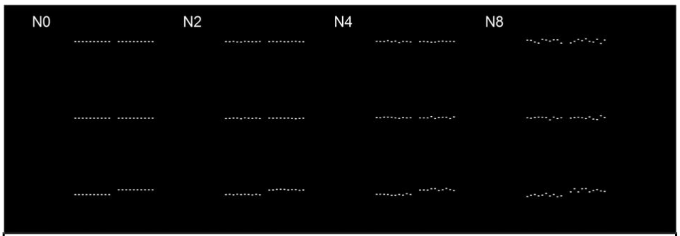


Figure 1 (left): *setup from Teng et al (2012) with d as the distance between setup and participant’s ear, x as the separation between disks and Θ as angle of separation to be detected.*

Figure 2 (above): *example of a vertical axis of differentiation often used in acuity tests of perception (source: http://www.nature.com/srep/2012/120305/ srep00300/fig_tab/srep00300_F1.html)*

The 6 expert human echolocator participants were divided in two groups of 3, one group at a distance d = 50 cm and one group at d = 100 cm from the experimental setup. A uniform surface was placed behind the setup at all experimental locations to exclude interference of differing backgrounds. A similar surface was placed between setup and participant each time the disks were being moved and the participant received a shoulder tap when it was allowed to start clicking and give a judgement about disk positioning. They received feedback following each trial, after which the disks are repositioned for the next trial.
A visual version of this set up was presented to 4 sighted individuals, 2 with good vision and 2 with good corrected vision through wearing glasses, who were presented 2 white disks against a uniform black background. The setup was placed more to the peripheral part of the eye, monocular under a 35° angle, since the acuity of the central part of the retina is extremely fine and under this angle, the visual acuity is expected to be more comparable to the auditory echoic acuity of the human echolocators. On average, the human echolocators could distinguish a 3.46° auditory angle above the

75% threshold, with the 3 best performers even below 2° at this threshold (Teng et al, 2012). This is more accurate than their own earlier study (3.76° angle, see also chapter 4), as well as other studies (Teng&Whitney, 2011; Thaler et al, 2011). The sighted participants achieved an average of 1.4° at the 75% threshold (under 35° eccentricity) which is comparable with the results of the best echolocator participants in this study. The researchers additionally state that the result is also comparable to or better than the results of artificial echolocation devices or sensory substitution devices. The 3 best performers had similar acuity to some natural echolocator species, like the big brown bat (Teng et al, 2012).

Background information of the participants further indicates that the better performance of the 3 best performing human echolocators could lie in the earlier blindness onset, which could indicate a greater adaptational ability to the younger brain, compared to the late onset blind participants.

*And of course it is difficult to reach this level of acuity in daily life, since the setup is stationary and on the same level as the head, with differences over the horizontal axis only, which is within the optimal range of hearing and echolocation performance. Differences over the vertical axis and a setup higher or lower than the head or placed at an angle towards the head would all cause a drop in accuracy up to varying degrees (Teng et al, 2012).

An interesting study on the ability of interception actions by human echolocators was performed by Vernat & Gordon (2010). The setup is an indirect interception design, so there is no direct contact between the target that needs to be intercepted and the participant. Instead, a ball (“interceptor ball”) is used as a mediator to hit the target, which is also a ball (“target ball”), rolling over a track of varying length and shape, thus varying the target’s speed as well (Slow, Mod, Fast). The launch track on which the participant rolls his ball towards the intersection (Pos-1) was also varied in length. In this way, the setup allows for testing the perception of moving objects and the ability to react on what is perceived. This perception-action paradigm has been performed earlier with sighted individuals and was found to be difficult to perform because of the variability in speed and acceleration of both the target and the intercepting ball.

To test the echo-delay effect, the whole setup was also placed closer (0.25m) or further (1.25m) away from a reverberant wall and the target track could be either horizontal or sloped, thus the target ball would decelerate (horizontal) or stay at a relatively constant velocity (sloped) on the track as shown in figure 3 below (left is horizontal, right is sloped; adapted from Vernat & Gordon, 2010).

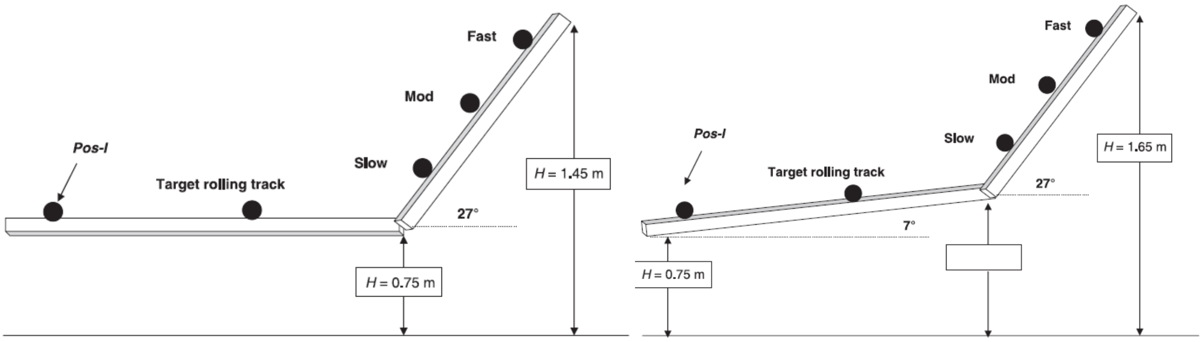


Figure 3: *schematic representations of the setup used by and adapted from Vernat & Gordon (2010).*

The researchers used 3 determinants:

1) Constant Error (CE), which is the time difference of target and interceptor ball at the intersection (Pos-1) as a measure of accuracy;

2) Launch Duration (LD), the time for the interceptor ball from leaving the participant’s hand to reach the intersection as a measure of the rolling speeds by a participant (and naturally the experimentally varied rolling distances are reflected in the LD as well);

3) Variable Error (VE) is the standard deviation of CE determined per individual participant and then pooled for every condition.

Based on the results, Vernat & Gordon (2010) suggest that the participants used a constant strategy for launching the interceptor ball, without variation in launch speed, thus making the speed and deceleration of the target ball the only variables. As such, it requires timing by the participants to let the target and interceptor balls collide (e.g. a low CE), a temporal determinant. However, the greater differences in the condition without deceleration (sloped) indicate a spatial cue to be a likely determinant, too, as the participants could decide on a specific point on the track for the target ball to reach before launching the interceptor.

The researchers point out that this is a difference with visual perception-action literature, where the primary explanation is visual *tau*. Visual *tau* is defined as:

$$\frac{\text{the size of the retinal image}}{\text{the rate of expansion of the image on the retina as it comes closer to the observer}}$$

They termed the auditory equivalent acoustic *tau*. Acoustic *tau* would use the same principal:

$$\frac{\text{intensity of the sound}}{\text{Sound increase due to the object coming closer to the observer}}$$

The variability in CE indicates that acoustic *tau* is not the primary explanation for accuracy, but shares this with spatial and temporal determinants.

The next research step would be to investigate active echolocation and movement, since passive echolocation and movement as well as active echolocation on motionless objects was studied previously. However, this would take a new design type, possibly combining elements from the different studies reviewed above. For example the study of Thaler et al. (2011) with fMRI might be difficult to perform with movement instead of static objects, but a further advanced version of Schörnich et al.'s (2012) virtual acoustic space could be developed to allow for virtual movement effects while the participant is static and could be placed in a fMRI scanner. Also, the experiment of Vernat & Gordon could be adapted to allow for active echolocation if the target does not move too fast and can be detectable in shape using a tongue click or other self-generated sound. This would require involvement of a human echolocation expert user from the start during the design of the experiment as well to explore the possibilities and impossibilities of a certain test and think of solutions to the problems that would arise. The role of acoustic *tau* in perception-action tasks could also increase with the use of active echolocation, since an equivalent of a mental image is created, which becomes larger in size as the object comes closer to the observer, making its function more similar to visual *tau* than with passive echolocation alone as Vernat & Gordon (2010) tested.

Analogy with animal studies in echolocation

Cognitive animal studies:

Knowledge of how echolocation works in other animals can give us more insight in the way human echolocation could work, how our brain processes echolocation or can adapt to its use and yield opportunities for improvement and optimization of the technique's use by humans.

Most well-known and studied are the many different types of bats. These many bat species have shown several ways of using echolocation and processing of the information.
Most similar to human echolocation are the frequency-modulated (FM) bats, which use short, sweeping downward FM sounds. Just like in humans using echolocation, as described in chapter 4, the spectrum is quite broad, thus ideally containing more information within the echo while covering a larger area, useful for navigational purposes. Some bat species are adapted to more cluttered environments, where wider sweeps can be confusing. These constant-frequency (CF)/FM bats prefer using a certain small constant frequency range and have specialized neurons and ear-acoustics for these frequencies, which results in an "acoustic fovea", using FM signals only in less cluttered and more convenient environments. Some of the CF species are specialized in interpreting the Doppler-shifts which can be detected when using CF and are even able to interpret overlapping sound pulses and echoes. Other CF species and FM bats are able to shorten their emitted pulses while closing in on their target in order to avoid pulse/echo overlap. The bat physiology allows for rapid and accurate modification of their echolocation signals, similar to the acuity of, for example, human speech.
Some of these adaptations are in the ear, apart from the outer ear, which is for bats often very big compared to the rest of the body, but most of the ear structure remains comparable to other mammals. However, the structure is more sensitive and detailed with the means of processing all this information in their brain to match. Additionally, bats are able to use the echoes of other bats to acquire more information about their surroundings as well (Airas, 2003).
Learning to shorten emitted pulses while closing in on a target is a technique which should be useable by human echolocators as well, albeit to a lesser extent than bats due to the physiology of both ears and larynx/tongue. Using the echoes and sounds of other echolocators when travelling in groups could likely also be learned to interpret, increasing overall team performance when navigating the world.

With respect to the underlying neurophysiology, Sayegh et al (2012) studied recovery cycles in the inferior colliculus (IC) in bats, as Hoshino&Kuriowa (2002) studied the IC in humans (see chapter 5). The percentage of duration-tuned neurons (DTNs) in humans, just like in cats and other non-echolocation species lies around 7%. Sayegh et al. found that in bats however, these DTNs are more abundantly present and have more different, specific and accurate functions, as they make up most of the distance map in the auditory cortex. DTNs are thought to be focal points for excitatory and inhibitory signals from both ears, arriving at different temporal intervals generating a spiking activation pattern in neurons based on echo-delay of specific tones. All DTNs have a certain state at which their spiking is at its maximum. Bandpass and Shortpass DTNs show maximal spiking at an optimum duration for that neuron. Bandpass DTNs spike counts fall below 50% at durations longer and shorter than optimum, while shortpass do so only for longer durations. Longpass DTNs do not have one optimum, but start spiking when stimulus exceeds a certain minimum duration. Sayegh and colleagues, using electrophysiology techniques, found that recovery times of non-duration sensitive IC neurons and Shortpass DTNs were significantly shorter than bandpass DTNs when the ear of bats was stimulated with two consecutive tones with increasing interpulse intervals. Since they found that even the shorter recovery cycles are longer than the difference of sound and echo at very short distances, they propose that DTNs might be sensitive to the additive stimulation of both pulse and echo paired together within the same recovery cycle reaching the neuron's optimum. This mechanism would also fit in nicely with the previously mentioned fact that bats are able to distinguish overlapping sound-echo combinations. However their results are not final and more research is needed to be decisive. How human IC neurons react to stimuli is also not clear yet, thus translation to human echolocation is still a few steps away. The mechanisms in bats are not deemed very different from other mammals by the authors, thus perhaps training to learn interpretation of overlapping sound-echo combinations for humans is possible in the long run (Sayegh et al, 2012).

Moss & Sinha (2003) modeled the pathways via which perceived input reaches the IC from the ears (and other senses) while passing through other brain areas. They included the neurotransmitters responsible for the interactions in the situations where these were identified (Figure 4). Additionally they review the first results on the system of echolocation motor control. Li & Yong (2007) build upon these results to model a simplified system of the combined and coupled sensorimotor mechanisms in echolocating bats (Figure 5).

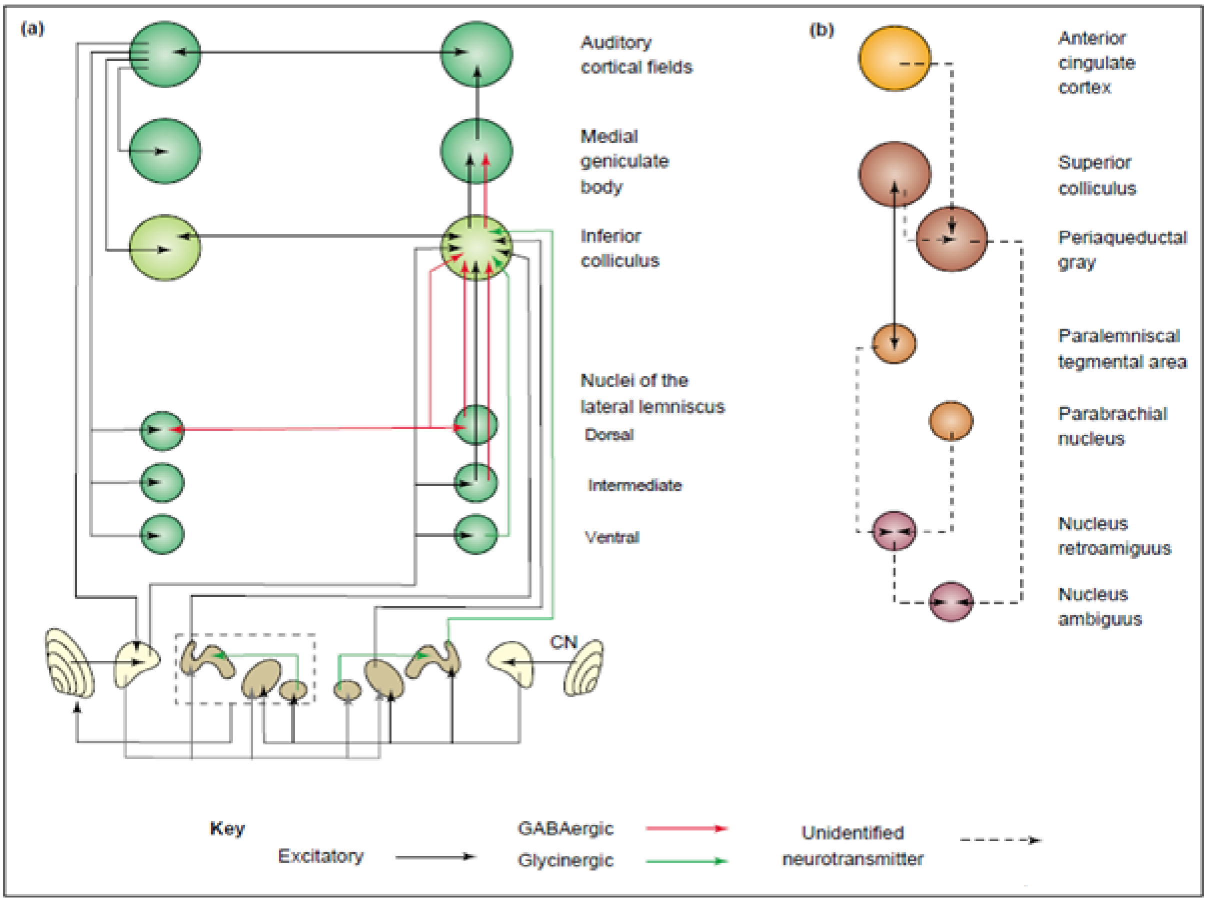
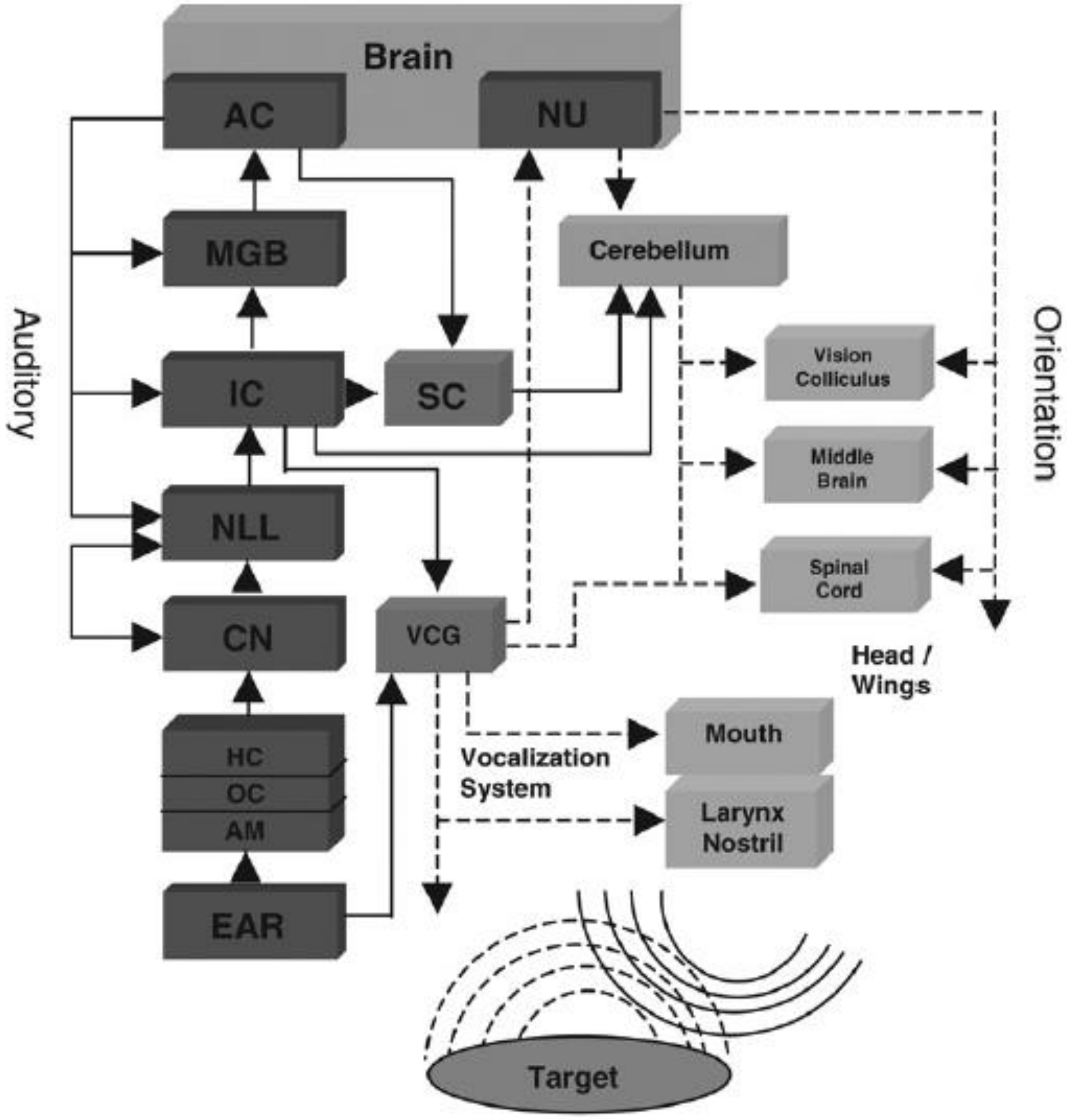


Figure 4 (above): *(a) the sensory processing interactions of echolocation signals, centered on the IC, originating from the cochlear nucleus (CN) and the auditory cortical fields received from the ears. Positive and negative feedback loops (red and green arrows are inhibitory) between the different brain areas allow for integration of the incoming information. (b) is the proto-model of the motor control system. Adapted from: Moss & Sinha (2003).*
Figure 5 (next page): *motor control of the bat. When navigating normally through the air, the Superior colliculus (SC) receives processed information from the IC and to a lesser extent other areas in order to determine the next set of movements. When flying at high speed close to a target, e.g. when hunting prey, the IC and SC integrate into a sensorimotor complex, enabling them to react and move much faster, in a more reflexive way through a fast feedback control loop. Abbreviations: AC = auditory cortex; MGB = medial geniculate body; NLL = nucleus of lateral lemniscus; hair cell; OC = ossicular chain; AM = auditory meatus; NU nucleus; VCG =vocal central gray matter. Adapted from: Li & Yong (2007).*



Hoffman et al. (2010) challenged the capabilities of the bat's auditory cortex by subjecting the animals to different inter-aural intensity differences (IID's) and inter-pulse intervals (IPI's). With these methods the researchers were able to distinguish which group of neurons in the auditory cortex is dedicated to focus targeting in the later stages of target pursuit., when the bat is close to its target. In these stages the integrated sensorimotor system combining information from IC and SC as described above by Li & Yong (2007) is active (Fig. 5). Hoffman et al (2010) found that a portion of the neuron receptive fields in the dorsal parts of the auditory cortex are focused on the target (up to 21%), while the other neurons are not and react to more peripheral surrounding input.

Object recognition was mentioned in chapter 2 as one of the more difficult skills to perform with echolocation. Research in bats by Genzel & Wiegrebe (2013) showed that shape detection and object recognition is independent of object size. Objects of different sizes falling within 1 of 2 object shape categories (Sphere vs hourglass) were presented to the bats in a Y shaped tunnel and bats were rewarded only when choosing the right object. For a second experiment, the echolocation signals used by the bats were recorded and transformed into human audible range. Artificial vowels were

created matching the transformed bat signals and presented to human listeners to compare the discrimination of object shape with bats in their first experiment.
The object identification differed between humans and bats per object type and scale, but on average showed a similar underlying identification system and method. Analysis of the signals and echoes indicate which echo properties are similar for different sizes of the same object shape. With decreasing size, amplitude decreases as well, time intervals compress and the spectral ripple (logarithmic scaled frequency pattern) expands, while the form stays the same. Therefore, the authors conclude that bats have some kind of internal reference representation of an object to which different scaled variations are compared and identified. Previous research in humans and the results from their second experiment indicate that a similar system is employed by the human brain as well (Genzel&Wiegrebe, 2013).

Genetic animal studies:

The studies discussed above are indicative of both differences and similarities between bats and humans. As such, it would be interesting to investigate these differences and similarities on a genetic level as well.
Although manipulation of human gene expression to enhance echolocation abilities would be rather controversial to say the least and difficult as well, it is still interesting to see how bats are genetically adapted to use echolocation. Enhanced mechanisms in bats might be aims for manufactured aids in the future as well and as such a few possibly relevant studies will be discussed here.

One gene family of interest is the connexins. Connexins form canals between cells which allow for the exchange of small molecules and ions. Different connexins are found in the brain and auditory system. Mice and other mammals connexins 26 (Cx26) and 30 (Cx30) have been found so far to be predominant in the cochlea and the only connexins present in the organ of Corti, with mutations in Cx26 being responsible for many cases of deafness and hearing impairment in Europe (Horowitz et al, 2008). However, Horowitz and colleagues (2008) discovered another connexin, Cx36, in the auditory system of bats as well, which is normally found in the retina of mammals and in various brain areas, but not in the cochlea. The researchers suspect that Cx36 in the cochlear nuclear complex enables "synchronization of spikes between cells tuned to different frequencies early in the central auditory system." (Horowitz et al, 2008). In a study by Liu et al (2009) Cx36 was also found in individual spiral ganglion neurons, which translate the stimuli from the cochlea to an actual action potential to be sent to the brain. They suggest, after Horowitz and colleagues' research, that a similar function of rapid integration of information before processing in the brain could be facilitated by the presence of Cx36, playing a role in human's ability to use more elaborate speech through the synchronization of action potentials (Liu et al, 2009).

Functional difference can be gained by adding a gene where other species do not have that gene, like Cx36, but changes specific for bats in genes that are present and highly conserved among species can be equally important. Almost all species (birds, reptiles, mammals, etc.) use vocalizations of some sort, but bats use it for echolocation as well. Li et al (2007&2008) studied 2 of these conserved genes, FoxP2 and Prestin, by means of large scale taxonomy studies and found many small differences and variations within the same genes. Most likely this allows the many different bat types to each have their own specific niche within the same environment, minimizing competition over the same resources. They speculate that the constant evolutionary pressure on these genes is the cause for the strong diversification of bat species and the different forms of echolocation (or the loss of echolocation in some bat species). This would be similar to FoxP2's association with the evolution of language, vocalizations and vocal learning in humans and Prestin's role in amplification of outer hair cell stimuli towards the brain in other mammals, adapted for usage of echolocation. They even conclude that possibly similar forms of high-frequency hearing and echolocation (CF) have evolved several times from the more basic FM sweep under different circumstances, but leading to a similar endpoint (Li et al, 2007; Li et al, 2008).

Finally, specialization of genes during evolution can lead to a greater extent of structural changes to enhance performance on a more macroscopic scale. An important example is the ear and outer ear canal of bats, which can take many different shapes. The ridges on the ear of one such bat species, the *E. fuscus*, which were previously thought to be present only for structural support, were modeled by Kuc (2009) to determine their acoustical function. The ridges are positioned in such a manner that they form a kind of acoustical paraboloidal lens, focusing divergent sound, redirecting the sounds as a beam into the ear canal, which greatly enhances the relative intensity of the sounds. Specifically high frequency sounds are filtered by these ridges, enabling high-frequency sensitive hair cells in the ear canal to perceive sounds, otherwise beyond hearing-range, if they are of sufficient intensity. The authors showed that the same is true for humans, by aiming a transmitter directly at the ear canal of a subject which generated a sound of 40 kHz. The subject was able to perceive the sound, but it sounded as 14 kHz, previously determined with hearing tests as the upper limit range of the subject. The sound vanished if the transmitter was turned away more than 20 degrees from the ear canal (Kuc, 2009).

The knowledge of these specializations in bats and other echolocating mammals can be used to improve teaching methods of human echolocation, as they give further insight in how sounds and their echoes are received, processed and perceived in the brain. Knowledge of structural changes can also be used in devices, for example high frequency clicking and receiving devices could enable human echolocators to shorten echo delay and latency. More research in the analogous field of animal studies on echolocation is clearly useful in understanding and improving human echolocation.

Conclusions and Discussion: influence of recent research on teaching human echolocation

In the previous chapters, it has become apparent what the strengths and weaknesses of echolocation are. An advantage is the possibility to train and learn how to use human echolocation to detect and navigate one's surroundings from a distance with a general, 360° all-around view, while Flash sonar allows for more detail when needed. Due to the concept of $\tau\alpha\upsilon$ not only static objects, but also movement is detectable, however a disadvantage is that high detail and object recognition are harder to perform with human echolocation and require a greater level of skill, training and experience with identification of different shapes and materials. Composition of the objects to be detected is important to familiarize with. In accordance with this, the properties of the self-generated sounds and active and passive echoes have been studied and discussed above. Research in both humans and bats on the way echo-acoustic information is processed in the brain gives more insight in the actual neural capabilities involved in echolocation and the possibilities of human echolocation.

Many of these more recent findings in research on human echolocation have not yet been implemented in the known teaching methods. Translation from research, especially fundamental and animal research, to use in practice is always challenging and for human echolocation this is no different. Often more research is needed before study outcomes can be used and therefore some possibilities for further research and even new directions will be discussed here as well.

To recapitulate, the three main factors for blind mobility were already mentioned in chapter 4:

1. Negotiating objects whilst avoiding bodily contact with the objects
2. The ability to stay on a path without accidental departure
3. The ability to cross streets or other open spaces quickly, efficiently, directly and safely without incident.

It is possible to approach the question how teaching human echolocation can be improved by recent research, as described in the previous chapters, from different angles:

1. (Behavioral) studies on human echolocation and applied general teaching studies
2. The Neural basis of echolocation and functional (imaging) research
3. Animal studies

1.) (Behavioral) studies on human echolocation and applied general teaching studies

Learning human echolocation involves re-learning how to listen. As seen in chapter 5, the visual cortex is activated when echolocating (Thaler et al, 2011), thus parallels with learning how to see can be drawn. Just like sight can be monocular and binocular, so we can listen monaurally and binaurally. Children with a dominant eye often get an eye patch to stimulate the latent eye. When both eyes are of equal strength again after some time, the binocular vision has improved. The same could be done with the ears, to test and train both ears monaurally, in order to improve binaural hearing, which is an important factor in human echolocation.
In chapter 5, Schörnich and colleagues' (2012) work shows that learning relative object distances is an effective way to give human echolocators the auditory equivalent of stereopsis through binaural detection of these multiple objects at various distances and angles.

It would be very interesting to follow the learning process in the brain as well. Comparing fMRI scans and neurophysiological methods like EEG over time could give us that information. Over a shorter period, students of the technique at different skill levels and experts can be compared, too. As an additional comparison, the same process could be followed over time in sighted people learning human echolocation or sighted people who have echolocated before (for example in earlier studies and experiments) can be compared with sighted people who are new to the technique.

An important part of teaching and learning in general is assessing what the students are doing and what they are capable of. A sighted instructor can mostly see how the student performs, but a blind expert echolocator, ideally also involved in the teaching process of the technique, might need different means of assessing the student's capabilities and progress. After considering how the instructors (both blind and sighted) can assess the student, consider how the student assesses himself and his fellow students. Key to the success of human echolocation is partly the increase in self-confidence of the student in his own capabilities. Recent research on teaching methods in the general education system suggests that conventional examinations are not the best way to build up this confidence nor effectively test the student's real capabilities or give adequate feedback for improvement. Instead, a shift to more peer-assessment is proposed in the field (Sadler, 2009; Race, 2013; Boud, 2010). The basis of this proposed learning strategy is that assessing how someone else is performing and having to formulate feedback gives you yourself a more in depth concept of the subject matter. Peer-assessment and making informed judgments on how your fellow students perform and giving feedback not only helps those students, but also develops the ability of self-assessment in a student while learning something. This learning strategy could be effective in teaching human echolocation as well as in the general education system.

2.) The Neural basis of echolocation and functional (imaging) research

A way to investigate the role of the visual cortex in human echolocation could be by temporary deactivation of brain areas found in the study of Thaler et al (2011) with transcranial magnetic stimulation (TMS) and test how this influences the performance of the different participants. Probably Early Blind and Late Blind participants will undergo different changes compared to each other and to sighted controls. This will test the causal involvement of these areas in echolocation (that is whether they are *necessary* for performing this function).

As suggested at the end of chapter 5, another next research step would be to investigate active echolocation and movement, since passive echolocation and movement as well as active echolocation on motionless objects was studied previously. However, this would take a new design type, possibly combining elements from the different studies reviewed in chapter 5. As said, the study of Thaler et al. (2011) with fMRI might be difficult to perform with movement instead of static object. The pre-released abstract on the internet of a manuscript of Schörnich and colleagues for this year (Schörnich et al, 2013), is a step in that direction. They continue the work on their virtual echo-acoustic space described in chapter 5 (Schörnich et al, 2012) and seem to have followed one of the directions already: involvement of expert echolocators from the start of experimental design, as Daniël Kish is one of the co-authors. They tested various psychophysical properties of human echolocation in their virtual echo-acoustic space with sighted participants and determined the resolution of the technique for different distances of the reference object (1m for a reference 3.4m or further away, 0.5 for a reference at 1.7m) as well as the ability to discriminate room-size changes (less than 10%). Continued research in this direction, especially while simulating movement, would be very interesting, while analyzing both in factors as accuracy and resolution or in terms of brain activation and changes.

3.) Animal studies

Learning to shorten emitted pulses while closing in on a target, as used by bats, is a technique which should be useable by human echolocators as well, albeit to a lesser extent due to differences in the physiology of both ears and larynx/tongue. Using the echoes and sounds of

other echolocators when travelling in groups can also be learned to interpret, increasing overall team performance when navigating the world.
Genzel & Wiegrebe’s (2013) results indicate that object recognition is independent of size and mainly determined by object shape, both in bats and humans. This knowledge can be used while teaching echolocation, by focusing more on object shape identification, since similar objects of different sizes will probably also be identifiable for the echolocator. General techniques of perceiving very small or very large objects of course still need to be taught in order to recognize shapes. The echolocator’s brain can subsequently compare the shape to the normalized sized shapes of objects and identify them.

Combining human echolocation with other tools and aids such as the white cane, a guide dog and/or SSDs (sensory substitution devices) will increase the effectiveness of each individual navigation method substantially. Thus far SSDs have not been able to outperform human echolocation by a considerable margin. However, they can be helpful in situations where echolocation (together with a white cane) falls short, since it is much easier to develop a SSD for a specific shortcoming than to outperform the combination of human echolocation with a white cane. A somewhat extreme example would be a specialized SSD to use echolocation/sonar underwater, like dolphins can, as suggested in chapter 2, or other conditions, environmental or otherwise, which make use of echolocation difficult.

Utilizing adaptations of echolocating mammals like bats (chapter 6) and dolphins (chapter 2) to develop and improve such devices could be helpful to further increase navigational performance. Similar to the proposed use of high frequency clicking and receiving devices in chapter 6, Uchibori and colleagues (2013, abstract of lecture) have very recently shown at a convention of the Acoustic society of America that they made it possible for sighted people to use and understand bat-like echolocation using a miniature dummy head by transposing loudspeaker sounds recorded by the miniature dummy head to audible pitch for humans and then playing them via headphones. Although still prone to errors, this could be shaped into an effective tool for human echolocators with more animal research and technological advancement of the device, to allow for specificity and accuracy closer to bat-like performance than human echolocation can currently achieve.

With the conclusive remarks above in mind, it becomes clear that research in recent years from various angles can contribute to the improvement of teaching human echolocation, as well as improving the technique and its use in combination with (technological) aids.

Acknowledgements

I want to thank Marten van Doorn and all the employees from Bartiméus whom I talked to during their echolocation workshop. Experiencing the technique first hand really shows the possibilities of the human echolocation technique better than words and explanations are able to do. Thanks to Tom de Witte and Daniel Kish for their workshop in Belgium as well, where the impact of the technique on the lives of blind and visually impaired users became clearer to me.
I also want to thank Chris Dijkerman for supervising and guiding the scientific side of my research and helping me to combine that with the practical experiences into words, written above.
And I want to thank all involved and the people around me for the discussions, most notably the participants of the Mind the Brain Symposium and my fellow students there, whose input I was able to use in writing this review article.
Lastly, thanks to Geert Ramakers and Pierre de Graan for allowing me to follow the intriguing spell of human echolocation that came over me, even though it is a bit off the beaten Track.

References

Airas, M., *Echolocation in Bats*, Proceedings of Spatial sound perception and reproduction, april 2003

Ammons, C.H., Worchel, P., & Dallenbach, K.M. (1953). "Facial Vision": The perception of obstacles out of doors by blindfolded and blindfolded-deafened subjects. American Journal of Psychology, 66 (4), 519-553.

Armstrong. (1975). Evaluation of Man-Machine Systems in the Mobility of the Visually Handicapped. in R.M. Pickett & T.J. Triggs (Eds.) Human Factors in Health Care. Lexington Books: Lexington.

Auvray, M., Hanneton, S. and O'Regan, J. K. (2007). Learning to Perceive with a Visuo-Auditory Substitution System: Localisation and Object Recognition with 'the vOICe' *Perception* 36, 416-430.

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, 938-949.

Boud, D. and Associates (2010). *Assessment 2020: Seven propositions for assessment reform in higher education*. Sydney: Australian Learning and Teaching Council.

Brozzoli C., Gentile G and Ehrsson HH. (2012). That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *J. Neurosci.* 32(42): 14573-14582.

Carlson-Smith C, Wiener WR (1996) The auditory skills necessary for echolocation: a new explanation. J Vis Impair Blind, 90(1):21–35

Ciselet V, Pequet E, Richard I, Veraart C, Meulders M (1982) Substitutionsensorielle de la vision par l’audition au moyen de capteurs d’information spatial. Arch Int Physiol Biochem 90: P47.

Cotzin, M. and Dallenbach, K.M. (1950). Facial Vision: The role of pitch and loudness in the perception of obstacles by the blind. American Journal of Psychology, 63 (4), 485-515.

Cotzin, M. (1942). The Role of Audible Frequencies in the Perception of Obstacles by the Blind. Psychological Bulletin, 39, 503-504.

Davies T. C., Pinder S. D. and Burns C. M. (2010). What’s that sound? Distance determination and aperture passage from ultrasound echoes. Disability and Rehabilitation: Assistive Technology, 6(6): 500-510

De Volder AG, Catalan-Ahumada M, Robert A, Bol A, Labar D, Coppens A, Michel C, Veraart C (1999) Changes in occipitalcortex activity in early blind humans using a sensory substitution device. Brain Res 826(1):128–134

Devore, S., Ihlefeld, A., Hancock, K., Shinn-Cunningham, B. and Delgutte, B. (2009). Accurate Sound Localization in Reverberant Environments is Mediated by Robust Encoding of Spatial Cues in the Auditory Midbrain *Neuron* 62, 123- 134.

Gagnon, L., Kupers, R. and Schneider, F. C. (2010). Tactile Maze Solving in Congenitally Blind Individuals *Neuroreport*. 21, 989-992.

Graziano, M. S., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845–859.

Genzel, D. & Wiegrebe, L. (2013). Size does not matter: size-invariant echo-acoustic object classification. J Comp Physiol A, 199: 159-168.

Griffin, D.R. (1986). Listening in the Dark: Acoustic orientation of bats and men. Comstock Publishing Associates, Ithaca, New York.

Guipponi, O., Wardak, C., Ibarrola, D., Comte, J.-C., Sappey-Marinier, D., Pinède, S., & Ben Hamed, S. (2013). Multimodal convergence within the intraparietal sulcus of the macaque monkey. *The Journal of neuroscience*, *33*(9), 4128–39.

Hayes, S.P. (1935). Facial Vision or the Sense of Obstacles. Perkins Publications, 12, Perkins Institution: Watertown, Mass.

Hemila, S., Nummela, S. and Reuter, T. (2010). Anatomy and Physics of the Exceptional Sensitivity of Dolphin Hearing (Odontoceti: Cetacea) *J. Comp. Physiol. A. Neuroethol Sens. Neural Behav. Physiol.*

Hoffmann, S., Schuller, G. and Firzlaff, U. (2010). Dynamic stimulation evokes spatially focused receptive fields in bat auditory cortex. European Journal of Neuroscience, 31: 371-385.

Horowitz, S. S., Stamper, S. A. and Simmons, J. A. (2008). Neuronal Connexin Expression in the Cochlear Nucleus of Big Brown Bats *Brain Res.* 1197, 76-84.

Hoshino, O. and Kuroiwa, K. (2002). A Neural Network Model of the Inferior Colliculus with Modifiable Lateral Inhibitory Synapses for Human Echolocation *Biol. Cybern.* 86, 231-240.

Johnson T (2012), Beginner's Guide to Echolocation for the Blind and Visually Impaired: Learning to See With Your Ears. Book

Kish D and Bleier H, 1994-2000. Echolocation: What It Is, and How It Can Be Tajght and Learned. *This material is adapted from Dan's Master's thesis entitled "Evaluation of an Echo-Mobility TrainingProgram for Young Blind People," and from presentations delivered by Dan to CAOMS in 1994, and Dan and Hannah to CTEVH and CAOMS in 2000.*

Kish D, (2003). Sonic Echolocation: A Modern Review and Synthesis of the Literature

Kuc, R. (2009). Model Predicts Bat Pinna Ridges Focus High Frequencies to Form Narrow Sensitivity Beams *J. Acoust. Soc. Am.* 125, 3454

Lee, D. N. (1976). A Theory of Visual Control of Braking Based on Information about Time-to-Collision *Perception* 5, 437-459.

Lee, D. N., van der Weel, F. R., Hitchcock, T., Matejowsky, E. and Pettigrew, J. D. (1992). Common Principle of Guidance by Echolocation and Vision *J. Comp. Physiol. A.* 171, 563-571.

Leonard, J.A. (1972). Studies in Blind Mobility. Applied Ergonomics, March, 37-46.

Li G, Wang J, Rossiter SJ, Jones G, Zhang S. (2007). Accelerated FoxP2 Evolution in Echolocating Bats. PLOS One,.

Li, G., Wang, J., Rossiter, S. J., Jones, G., Cotton, J. A. and Zhang, S. (2008). The Hearing Gene Prestin Reunites Echolocating Bats *Proceedings of the National Academy of Sciences* 105, 13959 <last_page> 13964.

Li, Y. & Song, Y.D. (2007). Neurophysiological study on sensorimotor control mechanism in superior colliculus of echolocating bat. ISA Transactions 46: 157-165.

Liu, W., Boström, M., Kinnefors, A. and Rask-Andersen, H. (2009). Unique Expression of Connexins in the Human Cochlea *Hear. Res.* 250, 55 - 62.

Moss, C.F. & Sinha, S. R. (2003). Neurobioogy of echolocation in bats. Current opinion in neurobiology, 13: 751-758.

Ono, H., Fay, A., and Tarbell, S.E. (1986). A "Visual" Explanation of Facial Vision. Psychological Research, 48 (2), 57-62.

Palakal, M. J. and Wong, D. (1999). Cortical Representation of Spatiotemporal Pattern of Firing Evoked by Echolocation Signals: Population Encoding of Target Features in Real Time *J. Acoust. Soc. Am.* 106, 479-490

Brown, S and Race, P (2012) *Using Effective Assessment to Promote Learning,* in *University Teaching in Focus: a learning-centred approach,* Hunt, L and Chalmers, D (eds), Australian Council for Educational Research and Routledge, pp.74-91.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behav Brain Res*, *2*(2), 147–163.
Rojas, J. A. M., Hermosilla, J. A., Montero, R. S. and Espí, P. L. L. (2009). Physical Analysis of several Organic Signals for Human Echolocation: Oral Vacuum Pulses *Acta Acustica united with Acustica* 95, 325 <last_page> 330.

Sadler, D R (2009) Indeterminacy in the use of preset criteria for assessment and grading. Assessment and Evaluation in Higher Education 34:2 159-179

Sayegh R, Aubie B, Fazel-Pour S, Faure PA (2012). Recovery cycle times of inferior colliculis neurons in the awake bat measured with spike counts and latencies. Frontiers in neural circuits, V.6 Art. 56.

Schenkman, B.N. & Jansson, G. (1986). The Detection and Localization of Objects by the Blind with the Aid of Long-Cane Tapping Sounds. Human Factors, 28 (5), 607-618.

Schenkman B. N. and Nilsson M. E., (2011). Human echolocation: pitch versus loudness information. Perception, 40(7): 840-52

Schenkman, B. N. and Nilsson, M. E. (2010). Human Echolocation: Blind and Sighted Persons' Ability to Detect Sounds Recorded in the Presence of a Reflecting Object *Perception* 39, 483-501.

Schörnich S, Nagy A and Wiegrebe L. (2012) Discovering your inner bat: Echo-acoustic target tanging in humans. JARO, s10162-012-0388-z.

Schörnich S, Wallmeier L, Gessele N, Nagy A, Schranner M, Kish D, Wiegrebe L. (2013) Psychophysics of human echolocation. Adv Exp Med Biol., 787: 311-9.

Stroffregen, T. A. and Pittenger, J. B. (1995). Human Echolocation as a Basic Form of Perception and Action *Ecological Psychology* 7, 181-216.

Supa, M., Cotzin, M., & Dallenbach, K.M. (1944). "Facial Vision": The perception of obstacles by the blind. American Journal of Psychology, 57 (2), 133-183.

Takahashi, T. T., Keller, C. H., Nelson, B. S., Spitzer, M. W., Bala, A. D. S. and Whitchurch, E. A. (2008; 2008). Object Localization in Cluttered Acoustical Environments *Biol. Cybern.* 98, 579 -586.

Teng S, Puri A, Whitney D, (2012). Ultrafine spatial acuity of brlind expert human echolocators. Exp Brain Res 216: 483-488

Teng, S. and Whitney, D. (2011). The Acuity of Echolocation: Spatial Resolution in the Sighted Compared to Expert Performance 2013.

Thaler L., Arnott S. R. and Goodale M.A. (2011). Neural Correlates of Natural Human Echolocation in Early and Late Blind Echolocation Experts. PLoS ONE 6(5): e20162.

Uchibori S, Kinoshita M, Ashihara K, Ohta T and Hiryu S. (2013). Human echolocation system using a miniature dumy head. J Acoust Soc Am.

Vernat J.P. and Gordon M.S., (2010). Indirect interception actions by blind and visually impaired perceivers: Echolocation for interceptive actions. Scandinavian Journal of Psychology, 51, 75-83.

Ward, J. and Meijer, P. (2009). Visual Experiences in the Blind Induced by an Auditory Sensory Substitution Device *Conscious. Cogn.*

Worchel, P. & Dallenbach, K.M. (1947). "Facial Vision": Perception of obstacles by the deaf-blind. American Journal of Psychology, 60, 502-553.