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Seeing with ears: how we create an auditory representation of space with echoes and its relation with other senses

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Abstract

Spatial perception is the capability that allows us to learn about the environment. All our senses are involved in creating a representation of the external world. When we create the representation of space we rely primarily on visual information, but it is the integration with the other senses that allows us a more global and truthful representation of it. While the influence of vision and the integration of different senses among each other in spatial perception has been widely investigated, many questions remain about the role of the acoustic system in space perception and how it can be influenced by the other senses. Give an answer to these questions on healthy people can help to better understand whether the same "rules" can be applied to, for example, people that have lost vision in the early stages of development. Understanding how spatial perception works in blind people from birth is essential to then develop rehabilitative methodologies or technologies to help these people to provide for lack of vision, since vision is the main source of spatial information.

For this reason, one of the main scientific objective of this thesis is to increase knowledge about auditory spatial perception in sighted and visually impaired people, thanks to the development of new tasks to assess spatial abilities. Moreover, I focus my attention on a recent investigative topic in humans, i.e. echolocation. Echolocation has a great potential in terms of improvement regarding space and navigation skills for people with visual disabilities. Several studies demonstrate how the use of this technique can be favorable in the absence of vision, both on the level perceptual level and also at the social level. Based in the importance of echolocation, we developed some tasks to test the ability of novice people and we undergo the participants to an echolocation training to see how long does it take to manage this technique (in simple task). Instead of using blind individuals, we decide to test the ability of novice sighted people to see whether technique is blind related or not and whether it is possible to create a representation of space using echolocation.

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Chapter 1

Spatial representation

Spatial perception is the capability that allows us to learn about the environment. All our senses are involved in creating a representation of the external world. In this work, we will review the literature regarding how the senses integrate among each other to create this representation of space and two cases of spatial representation: in case of blindness and using sounds to infer space, thanks to echolocation. Later on, we will present some original studies to investigate these topics.

1.1 Spatial representation in a multisensory environment.

1.1.1 Spatial representation and multisensory integration

Spatial representation is the results of the interaction between different modalities including vision, somato-proprioception, audition. The integration of this sensory information is a strategy to provide complementary information of the external world (Burr and Alais, 2006; Ernst and Bülthoff, 2004; Newell et al., 2010).

From electrophysiological studies in animals, it has been shown that the superior colliculus plays an important role in multisensory integration. Such low-level structure receives visual, auditory and somato-sensory inputs, that go to elicit the bimodal (and also trimodal) neurons. The receptive fields of the neuron overlap so that each neuron respond to stimuli come from the same portion of space and provide a functional map of external space (Meredith et al., 1991).The outcome behaviors, as the integration between the stimuli, will be faster and more accurate when all the three rules are respected, conversely, the reaction will be slower and less accurate to spatially discriminate stimuli (Calvert et al., 2004). An example of this continuous interaction between the senses is given by the phenomenon of adaptation and the possibility to transfer it among modalities, leading to cross-modal aftereffects. Konkle et al. (2009), by using a motion adaptation paradigm, found that exposure to visual motion stimulus in a given direction produces a tactile motion aftereffect, in which the person perceived illusory motion across the finger in the opposite direction of the visually adapted motion stimulus. They also observed that the aftereffect could be transferred from touch to vision, demonstrating that the processing of visual and tactile motion relies on shared representations that dynamically impact on modality-specific perception. Cross-modal interactions of a similar kind have been shown by visually induced aftereffects also in other sensory modalities, such as vestibular/proprioceptive (Cuturi and Macneilage, 2014) and auditory (Kitagawa and Ichihara, 2002).

When an ambiguity is present in the main modality involved in the perceptual experience, the complementary component may be sufficient to overcome the ambiguity and maintain stable the percept (van Ee et al., 2009). In other cases, the percept can be entirely modified, as in the so-called bounce illusion (Sekuler et al., 1997). In this illusion, there are two identical objects moving along a diagonal of a 2D display, and two objects appear crossing along a stream. However, when the two objects collide and a brief sound is simultaneously presented, the visual perception is biased toward the bouncing motion, i.e. the two objects seem to collide and rebound in the opposite direction to the initial trajectory.

Regarding spatial representation, the visual system is considered the most accurate sense for space judgments and the more influential modality for cross-modal calibration of spatial perception during development (Gori et al., 2012). Many studies support this idea, showing that when there is an incongruence between the spatial locations of for example audio and visual stimuli, vision usually dominates, causing the so-called “ventriloquist effect” (Alais and Burr, 2004; Mateeff et al., 1985; Warren et al., 1981). During the ventriloquist effect, the auditory stimulus is “captured” by the visual system, making us perceived the sound in the same location of the visual stimulus. The ventriloquist effect has been explained as the result of optimal cue-combination where each cue is weighted according to its statistical reliability. Vision dominates the perceived location because it is more reliable then audition in spatial judgments (Alais and Burr, 2004). Interestingly, vision can influence auditory space perception even when a visual stimulus is not directly involved in the auditory task. For example, performance in an auditory angle acuity task improves when vision is also present, even if are presented only auditory cues (Jackson, 1953; Shelton and Searle, 1980). A recent study by Tabry et al. (2013) has shown that the mere possibility of observing the setup by keeping eyes open during auditory horizontal and vertical localization tasks can improve audio accuracy, even if no visual cues of the stimuli are provided.

1.1.2. Different ways to represent space among sensory modalities.

Besides studying “how” the information is processed by the senses, it is interesting to investigate “where” this information is located in the environment before to be processed. The sensory input can come from the body or from outside, and in the latter case, it can be interpreted using different reference systems. So speaking about space representation, it is necessary to introduce the concept of the reference frame.

The frame of reference defines the coordinate with which space is represented (McCloskey and Rapp, 2001). It is possible to identify two main classes of the frame of references: egocentric and allocentric (Galati et al., 2010; Klatzky, 1998). The egocentric frame of reference means to represent the location of external objects with respect to the position of the body segments and provides a framework for goal-directed actions such as avoiding obstacles while walking and reaching objects. In contrast, the allocentric frame of reference refers to a framework independent of the body position, and it is constituted by object-to-object relations.

Several neuropsychological and neurophysiological studies provided evidence of anatomically and functionally different neural circuits underpinning allocentric and egocentric spatial coding. Same behavioral findings are provided by unilateral spatial neglect (Caramazza and Hillis, 1990; Heilman et al., 1983; Hillis et al., 1998; Ladavas, 1987). In the viewer neglect, the overlook of an object is independent of its relative position but concern just the contro-lesional side of the patient. On the contrary, the body related neglect indicates an impairment of the allocentric frame of reference. Two studies have described two patients confirming this dissociation: one showing body-centered neglect, where the processing of object-based spatial processing was intact, and the other patient showed object-centered neglect while there was no impairment of body-centered spatial processing (Hillis and Rapp, 1998; Ota et al., 2003). At the neural level, it has been suggested that the two information, egocentric and allocentric, are processed in parallel by the parietal lobe and the hippocampal formation, with eventual transfer to the hippocampus for long-term storage in allocentric coordinates (Feigenbaum and Morris, 2004; Kesner, 2000).

Another way to distinguish spatial perception, it is represented by how we react to the external item, that defines a peri- and extrapersonal space. Several lines of evidence show that our brain continuously generates multiple neural representations of coexisting spaces, depending on incoming sensory inputs, action/intention, and reference frames (Holmes and Spence, 2004; McNaughton and Nadel, 1990; Pasqualotto et al., 2013b). An interesting spatial representation, which is nowadays attracting a renewed interest is the peripersonal space (PPS), i.e. space immediately surrounding the body (Cléry et al., 2015; Dijkerman and Farnè, 2015; Ladavas and Serino, 2008; Rizzolatti et al., 1997; Serino, 2016). An extensive amount of studies showed that PPS is represented via the integration of somatosensory stimuli from the body with visual (Làdavas et al., 1998; Macaluso and Maravita, 2010) or auditory stimuli (Occelli et al., 2011) coming from the environment, when it is presented at a limited distance from the body, which defines the extent of the PPS. Interestingly, PPS representation has a direct link to the motor system, as stimuli presented within the PPS primes defensive (Graziano and Cooke, 2006) or approaching (Rizzolatti et al., 1997) body actions (Avenanti et al., 2012; Cardinali et al., 2009; Makin et al., 2009; Serino et al., 2009). When an item is presented in this portion of space the person tends to react faster comparing to further positions (extra-personal space). An important property of PPS representation is that it is dynamically modified through experience, i.e., by short (Canzoneri et al., 2013; Farnè and Làdavas, 2000; Holmes et al., 2004; Holmes and Spence, 2004) and long term (Serino et al., 2007) tool use, social interaction (Ferri et al., 2013; Heed et al., 2010; Teneggi et al., 2013) and potential movements (Brozzoli et al., 2010; Noel et al., 2015). PPS seems to have an adaptive role in order to support appropriate motor behaviors.

1.2 Two cases of spatial representation in atypical situations.

1.2.1 Spatial representation and visual impairment

As we seen in the previous paragraph, vision is the most accurate sense to estimate spatial information. Vision influences the other senses during spatial judgment, when for example two information are in conflict or after adaptation. Since the human brain relies so much on visual information, an interesting question is what happens to spatial representation when the vision is not available?

Congenitally blind individuals provide an excellent example of how our brain compensates for the lack of vision and how the experience might shape auditory processing regarding spatial perception. Until a few years ago the predominant hypothesis to explain the spatial performance of blind individuals was the “Compensatory hypothesis ”.

According to this view, the loss of vision is compensated by the intact sensory systems that are recruited to process spatial information and to develop an accurate sense of space (Collignon and De Volder, 2009; Hötting and Röder, 2009). This reorganization manifests itself at a behavioral level in enhanced performance of blind individuals, compared to sighted, in the tactile and auditory domain. About the tactile domain, it was shown that blind individuals are better than sighted in discriminating grating orientation (Goldreich and Kanics, 2003) and 2D angles (Alary et al., 2009), size discrimination with a cane (Sunanto and Nakata, 1998) and more in general in object exploration (Alary et al., 2009; Van Boven et al., 2000; Legge et al., 2008; Morrongiello et al., 1994).

Furthermore, several studies showed enhanced performance also in the auditory domain. For example, blind people are better performers in discrimination sounds pitch (Eschenbach, 2004; Gougoux et al., 2004).

The majority of the studies regard sound localization. It has been shown that blind individuals show enhanced monaural localization performance compared to sighted people (Doucet et al., 2005; Gougoux et al., 2004; Lessard et al., 1998), in particular in the peripheral auditory field (Röder et al., 1999), and for relative distance discrimination (Kolarik et al., 2013; Voss et al., 2004).

To support this hypothesis and the behavioral results, several studies showed a crossmodal plasticity, which exhibit thanks to an activation of the cortical visual areas in early blind individuals during auditory (for a review Collignon et al., 2009b; Gougoux et al., 2005; Renier et al., 2014; Weeks et al., 2000) and tactile tasks (Cohen et al., 1997; Sadato et al., 2002).

These enhanced performances are likely caused by a reorganization at the level of the cerebral cortex, characterized by a colonization of the neural areas by the intact senses, normally designated for visual processing. As regard enhancement in auditory perception, it has been theorized that it reflects the recruitment of visual cortex (Striem-Amit et al., 2012, 2015; Striem-Amit and Amedi, 2014; Weeks et al., 2000). This recruitment of visual areas is supported by studies showing that accuracy in auditory localization tasks correlates with the magnitude of visual cortical activation (Gougoux et al., 2005; Voss et al., 2011), implying that the more visual regions are recruited, the more auditory accuracy increase. A fine example is provided by a work of Collignon at al. (2009a) in which they applied transcranial magnetic stimulation (TMS) at the level of the visual cortex of blind participants while they performed a sound localization task. They showed that when the TMS was applied to the occipital cortex the participants' performance was spoiled, on the contrary when it was applied on the region critical for spatial processing of sounds (intra-parietal sulcus) the performance did not change.

The idea is that since blind people rely more on their hearing to acquire knowledge of the environment and navigate, it is likely that they acquire an expertise in using the auditory sense for spatial information causing a reorganization at the cerebral level in which areas that no longer carry their main function are colonized by others.

In the last few years, another theory has emerged to explain blind spatial performance, the so-called "General-loss" hypothesis.

This theory argues that vision is the only sense to encode spatial information, therefore the lack of vision does not allow blind individuals to develop a correct spatial representation (Eimer, 2004). In favor, several studies have shown that congenitally blind people are not able to perform specific auditory tasks, such as the space bisection (Gori et al., 2014a; Vercillo et al., 2016), reproduction of moving sounds (Finocchietti et al., 2015), vertical localization (Lewald, 2002; Voss et al., 2015; Zwiers et al., 2001) and distance discrimination (Cappagli et al., 2015; Kolarik et al., 2013). This hypothesis is supported by neurophysiological evidence in animals that visual feedback plays an important role for auditory spatial learning (Heffner and Heffner, 1992; King et al., 1988; Knudsen and Brainard, 1991) and for the normal development of acoustic spatial maps in the superior colliculus (King and Carlile, 1993; Knudsen, 1983). Indeed, in this case, the auditory map is continuously refined by visual experience so that during the development it becomes aligned with the representation of visual space (King, 2009).

Despite all the experimental results the role of vision in the development of spatial cognition is still unclear due to the high controversy among the results.

The "*General loss*" hypothesis goes to highlight the fact that the spatial deficits in blind are task-dependent and cannot undergo a generalization of the deficit or improvement. Consistent with this view, Gori et al. (2008, 2014a) proposed a cross-sensory calibration hypothesis that integrates the two current theories (Compensatory and General loss hypothesis). The idea is that during development the visual system calibrates the other senses to process specific aspects of spatial information due to the fact that vision is the most accurate sense to perceive spatial properties of the environment. Consequently, the lack of vision during the early stages of development does not allow the remain senses to benefit from the visual experience. In other words, audition and touch can learn from vision how to perceive space, and this calibration process must take place during early years of life, because if loss of vision occurs within the critical period, the full development of spatial cognition is compromised, leaving the blind to the possibility of performing only simple spatial tasks. Collignon and colleagues (2015) found that even after a short period of visual deprivation, during the early sensitive period of brain development, are present alterations of auditory-driven activity in occipital regions even after years of visual experience.

It has been shown that congenitally blind present an impairment in performing auditory space bisection but not an auditory discrimination task (Gori et al., 2014a). Moreover, congenitally blind are not able to reproduce the trajectory of a moving sound showing a deficit in the lower portion of space investigated, instead sighted and late blind do not show such impairment (Finocchietti et al., 2015). It seems that blind people are more challenged in performing task requiring an allocentric frame of reference in which it is needed the ability to put in relation the position of external objects among each other, while they have no problem to relate their own position with an object (Gori et al., 2014a; Pasqualotto et al., 2013b; Pasqualotto and Proulx, 2012). There are also neurophysiological studies supporting the visual calibration hypothesis, come from animal studies, showing that vision guides the maturation of auditory spatial response properties of neurons of the superior colliculus (King et al., 1988; King and Carlile, 1993; Knudsen, 1983; Knudsen and Brainard, 1991).

1.2.2 Human echolocation.

Echolocation is a biological sonar used by some animals, such as dolphins and bats, to navigate and hunt in environments where vision only is not enough to acquire spatial information. These animals produce self-generated sounds and are able to measure the time delay between their own sound emission and the reflections of that signals by the environment to infer spatial information and understand whether are present or no other animals or objects. The information about the horizontal angle from which the reflected sounds arrive are influenced by two component: the relative intensity of the sound received by each ear; and the time delay between the production of the sound and the path that the sound has to do to go back to the two ears.

Interestingly, some blind individuals have developed, by their own, this skill and use it mainly, as the other animals, to navigate and detect silent objects in the environment (for reviews see Kolarik et al., 2014; Thaler and Goodale, 2016). In the last few years, a growing number of studies started to show interest in understanding the behavioral application of echolocation as well as the neural bases of the echoes processing.

The first reason of this interest is that developing the ability to echolocate can offer real-life advantages for blind people, fostering social inclusion: echolocation is associated with higher salary and mobility in unfamiliar places, providing evidence that echolocation may play a role in successful adaptation to vision loss (Thaler, 2013).

Secondly, the new outcomes on the topic are pointed out in the direction of echolocation as the connection between audio-spatial and visuospatial information and consider echolocation an alternative way to provide spatial information and a good substitute for vision allowing a self-calibration of the auditory system in congenitally blind individuals. Moreover, it is providing an example of neuroplasticity, providing researchers a new paradigm for exploring how the brain deals with novel sensory information.

A behavioral evidence is furnished by Vercillo at al. (2014), where they compared the performance of blind expert echolocators, congenitally blind and sighted people, these last two groups with no previous experience of echolocation, in a complex space auditory task (space bisection). It was found that, contrarily to blind nonexpert echolocators, blind expert echolocators performed the spatial task with similar or even better precision and accuracy than the sighted group. This supports the hypothesis that echolocation recalibrates and even refines the ability of blind individuals to represent sounds in complex spatial configurations and compensate the lack of vision. Furthermore, other studies have shown that expert echolocators are susceptible to some properties particular to the visual system, such as size constancy (Milne et al., 2014a). 'Size constancy' is a perceptual phenomenon in which objects appear to be the same physical size independent of the size of the visual angle subtended (which changes with distance). The findings that blind expert echolocators can discriminate among objects based on their physical size (regardless of their 'acoustic size') suggests that size constancy may also operate during echolocation.

Studies concerning human echolocation focused on four main topics: distance and size discrimination, localization and navigation.

One of the main use of echolocation is navigation, and distance discrimination is fundamental for avoid collision (Supa et al., 1944). Using virtual acoustic environment, it was found that sighted people were able to use echolocation to detect an object at different distances (Schörnich et al., 2012). In other studies, it was investigated how some acoustic information (loudness and pitch) could influence the ability to detect an object at different distances (100, 200 and 300 cm). It was found that as long as the pitch component was present, listeners were able to perform the task and that there was a strong effect of distance, i.e. the participants' performance decreased with increasing distance, highlighting the importance of repetition of pitch for close distances, less than 2m (Schenkman and Nilsson, 2011). In another study, where participants had to identify right-versus-left lateral position task (Rowan et al., 2013), using recorded noise, was found the same result. It was highlighted that from distances of 2m or more, the participants' performance was random. Moreover, it was suggested that performance was due to high-frequency cues and longer auditory signals (400 ms), that improve performance compared to short signals (10 ms), at least for a distance below 1m. About depth perception with echolocation has been demonstrated that sighted people can distinguish the presence or not of an object at different depths mainly using recorded clicks or burst noise and in controlled environments (anechoic chambers or virtual reality). What is missing is to understand which is the environmental contribution for this type of task and which is the ability of discrimination within shorter distances using self-generated clicks.

The second aspect investigated regarding echolocation is localization (and auditory acuity). Thaler et al. (2011) found that expert echolocators are able to detect a change of around 4 degrees in the azimuthal position of a pole in a two-alternative forced choice. Moreover, Teng (2012) estimated that on average expert echolocators discriminate the presence of two objects in front of them (at 50 or 100 cm away) with 3.4 degrees of distance between the two objects (Echolocation Vernier acuity test). Impressively, one of the echolocators tested had a threshold of 1.22 degrees at 100 cm, that is quite comparable with visual acuity. The same test was performed also by sighted people that were able to perform such a task at 50 cm of distance after four/five session of training (Teng, 2011).

The third echolocation ability investigated was size discrimination. Teng and Whitney (Teng, 2011) found that the ability to perform a size discrimination task using echolocation is not related to the absolute stimulus size or distance, rather to the difference in auditory angle subtended by the stimuli. A couple of years later Thaler and al. (2014b) replicated the same experiment confirm the same results, i.e. sighted people are able to perform a size discrimination task using echolocation, but they added another component to the puzzle, finding that the ability to echolocate is related to the vividness of visual imagery.

Strictly related to the other three points are all the studies about navigation. Rosenblum et al. (2010) showed how sighted blindfolded participants were able to detect and walk up to an estimated position of a wall, finding that participants were more accurate when emitting sounds during motion than when standing still, for some distances. Kolarik et al. (2016), assessed the ability of blindfolded sighted people to detect and circumvent an obstacle just using mouth click sounds, compared to visual guidance. They showed that auditory information was sufficient to guide participants around the obstacle without collision, but there was an increase of movement time and the number of velocity corrections compared to visual guidance. Moreover, in a second study, Kolarik et al. (2017), used the same task to compare the performance between blindfolded sighted, blind non-echolocators and one blind echolocator using self-generated sounds and an electronic sensory substitution device (SSD). They found that using audition, blind non-echolocators navigated better than blindfolded sighted with fewer collisions, lower movements times, fewer velocity corrections and greater obstacle detection range. Instead, the performance using an SSD between the two groups was comparable. The expert echolocator had similar or better performance than the other two groups using audition but was comparable to the other groups using SSD. All these findings support the hypothesis of *enhancement*: vision loss leads to enhanced auditory spatial ability due to an extensive experience and reliance on auditory information (Kolarik et al., 2013; Voss et al., 2015) and cortical reorganization (Collignon et al., 2013; Kupers and Ptito, 2014; Voss and Zatorre, 2012). Another important point is that the head during echolocation seems to have a crucial role (Milne et al., 2014b). Wallmeier and Wiegrebe (2014a), showed how head rotations during echolocation can improve performance in a complex environmental setting. They also reported that during echolocation participants tend to orient the body and head towards a specific location (Wallmeier and Wiegrebe, 2014b).

At the beginning of the paragraph, we talked about the fact that echolocation can by alternative methods to study brain plasticity, i.e. investigate how the brain has reorganized after the use of this technique. One of the first studies to measure the brain activity during echolocation was performed by Thaler and colleagues (2011). They found an increased activity of the visual cortex for the recording contained echolocation clicks and echoes, and not in the sighted controls nor when participants were listening recordings with the clicks, but without echoes. In a second study, Arnott and colleagues (2013) found activity in ventrolateral occipital areas and the bilateral occipital. The interesting part was that they found a stronger echoes activation coming from the contralateral areas with respect to the position of the object and that the pattern of activation changed when the echoes moved away from the center toward the periphery of space. Furthermore, in a path direction during the walking task (Fiehler et al., 2015), it was found that both blind and sighted people show activation in the posterior parietal cortex during echolocation and the location of this activation might coincide with dorsal-stream areas involved in the processing of vision for motor action.

1.3 Objective of the thesis

To summary, we talked about how spatial representation is important to understand the world surrounding us. When we create the representation of space we rely primarily on visual information, but it is the integration with the other senses that allows us a more global and truthful representation of it. While the influence of vision and the integration of different senses among each other in spatial perception has been widely investigated, many questions remain about the role of the acoustic system in space perception and how it can be influenced by the other senses: which are the process underlying the interaction between the acoustic system and the other senses in auditory spatial perception? Can it be asserted that this improvement is due to a transfer of information from one system to the other? Whether it is true, which are the information transferred?. For this reason we deepen which is the role of the auditory system in spatial representation in sighted people and how vision and touch can *indirectly* influence auditory space perception. For this reason, we tested sighted participants during an auditory spatial task in different environments at the acoustical level and manipulating their knowledge of the environments using vision and touch.

Give an answer to these questions on healthy people can help to better understand whether the same "rules" can be applied to, for example, people that have lost vision in the early stages of development. Understanding how spatial perception works in blind people from birth is essential to then develop rehabilitative methodologies or technologies to help these people to provide for lack of vision, since vision is the main source of spatial information. As mentioned above, the literature concerning the acoustic spatial abilities in the blind is not clear about blind performance, because based on the kind of task is performed, the performance present enhancements and deficits. (Cappagli and Gori, 2016; Collignon et al., 2006; Goldreich and Kanics, 2003; Gougoux et al., 2005; Gurtubay-Antolin and Rodríguez-Fornells, 2017; Vercillo et al., 2016; Voss et al., 2004, 2015). It has been hypothesized that the discrepancy observed in these results concerning the spatial performance of blind individuals might be due to several factors, such as the spatial dimension, the frame of reference and the onset of blindness. In this thesis we focus the attention of the frame of reference used to judge the location of sound sources in space. The idea is that congenital blind individuals might have a deficit in remapping the space from egocentric to allocentric coordinates. To add a new piece of information, we have developed some tasks that are going to create a dissociation in the use of a frame of reference: body-centered or external.

The third subject take into account is echolocation. Echolocation is a topic of recent investigative interest in humans, because it has a great potential in terms of improvement regarding space and navigation skills for people with visual disabilities. Several studies demonstrate how the use of this technique can be favorable in the absence of vision, both on the level perceptual level, because it seems to help in the building of a spatial mental representation similar to that acquired through vision (Vercillo et al., 2014) and also at the social level, because it is associated with higher salary and mobility in unfamiliar places (Thaler, 2013). Based in the importance of echolocation, we developed some tasks to test the ability of novice people and we undergo the participants to an echolocation training to see how long does it take to manage this technique (in simple task). Instead of using blind individuals, we decide to test the ability of novice sighted people to see whether technique is blind related or not and whether it is possible to create a representation of space using echolocation.

. In particular, we have studied how it is possible to obtain information on depth and how to orientate our-self during navigation. Moreover, we have investigated how echolocation can affect multisensory integration.

To conclude, our results will show how spatial representation is dynamic and adaptable to both short and long-term contexts.

Chapter 2

Sensory interaction on spatial representations.

2.1 Spatial representation in sighted individuals

As it stems from the interaction between audio, vision, and touch, we can create a representation of the space surrounding us. Based on the information we receive, our perception may not correspond to what actually happens. An example is provided when we see a ventriloquist and his puppet: even if we know that the voice of the puppet is produced by a man, we perceive the sound coming from the moving lips of the puppet. The same effect has been reproduced also in laboratory and several studies during the past years have shown that vision is the most accurate sense to estimate spatial properties, as it dominates over the other senses in presence of incongruent information between senses (Alais and Burr, 2004; Ernst and Banks, 2002; Landy et al., 2012; Mateeff et al., 1985; Warren et al., 1981). Along with that, several studies have demonstrated, at a perceptual level, that auditory space perception can also be biased by tactile stimuli. Similarly to the audio-visual Ventriloquist effect, auditory localization seems biased toward the side of the concurrent tactile stimulus in bimodal tasks (Bruns et al., 2011; Bruns and Röder, 2010a; Caclin et al., 2002). Specifically, tactile stimulation influences the auditory cortical activity through higher areas assigned to the multimodal association (Bruns and Röder, 2010a).

Vision seems to be informative about spatial representation also for conditions in which visual inputs are not present during the auditory tasks (Jackson, 1953; Shelton and Searle, 1980; Tabry et al., 2013), improving the performance compared to performance when the participants were blindfolded. For example Tabry et al. (2013) during spatial localization performance increase if participants are allowed to look the experimental set up during the task comparing when they were blindfolded. Several questions arise: what is the process underlying this interaction? Can it be asserted that this improvement is due to a transfer of information from the visual to the auditory system? Which is the information that is transferred? Is it task-specific? Can be this improvement mediated by other senses such as touch?

2.1.1 How environmental observation influence auditory spatial perception

To answer the questions previously raised about the underpinning relation between vision and audition, in this study we investigate acoustic precision in sighted blindfolded participants in two audio tasks - minimum audible angle (MAA) and space bisection - and in two acoustically environments (normal room and anechoic room). We used these two tasks because require two different mental representation of space. The MAA is relative simpler than the space bisection because the participant had to compare the positions of the sounds with the position of his/her own body. Instead, in the space bisection to encode the position of the three sounds, and compare each position with that of the other sounds. While the space bisection requires a Euclidian representation of space and involves higher abstraction capabilities, for the MMA task a topological representation of space is sufficient (Gori et al., 2014a). The interesting part of this study was that participants had no previous knowledge of the structure of the room where the tasks were performed. We found an improvement of precision in the space bisection task but not in the MAA after the observation of a normal room. No improvement was found when performing the same task in an anechoic chamber. In addition, no difference was found between a condition of short environment observation and a condition of full vision during the whole experimental session. Our results suggest that even short-term environmental observation can calibrate auditory spatial performance. The idea is that the just a brief observation helps to create a mental representation of the place where the task is performed that improved the degree of reliability of the metric of the environment, thanks to a calibration due to vision. The results also suggest that echoes can be the cue that underpins visual calibration. Echoes may mediate the transfer of information from the visual to the auditory system.

Participants

Thirty-three healthy participant with normal or corrected to normal vision participated in the experiment (18 females, average age of 28, SD = ± 5). All participants gave informed consent in accordance with the Declaration of Helsinki before starting the tests. The study was approved by the ethics committee of the local health service (*Comitato etico, ASL 3, Genova*).

Procedure and apparatus

All participants performed two audio spatial tasks: an auditory space bisection task and a minimum audible angle (MAA) task. In the space bisection task, the participants heard three consecutive sounds and had to report verbally whether the second sound was spatially closer to the first (produced always by the first loudspeaker on the left) or to the third sound (produced always by the last loudspeaker on the right). The MAA task consisted of hearing two sounds and the participants had to verbally report which of the two sounds was more to the right.

The entire group of participants was divided into three smaller groups composed of 11 participants each. The first and the second groups performed four audio tasks (twice the space bisection and twice the MAA), the difference between the two groups was that the first group performed the task in an anechoic chamber (3m x 5m), instead the second in a normal reverberant room (7.2 m x 3.5). The participants of both groups were blindfolded before entering the room, so that had no knowledge of the environment or the set-up during the first two audio tasks (one space bisection and one MAA). After performing both tasks, the participants were allowed to remove the blindfold and observe the room for 1 minute: in one case an anechoic chamber (first group) and in the other case a normal room (second group). Afterwards, they were blindfolded again to repeat both audio tasks a second time. The third group was not blindfolded during the task, so they had full vision of the room and the set-up. They performed two audio tasks (once the space bisection and once the MAA). For all the groups the space bisection and MAA tasks were presented in a random order and each participant performed 60 trials for both tasks for each repetition.

The set-up was composed of an array of 23 loudspeakers, long 161 cm (Figure 2-**1**) and spanning ±25° of visual angle. The participant was sat in front of the center of the array at a distance of 180cm. During the auditory space bisection task, three stimuli, each having a duration of 75 ms, were presented at an interval of 500 ms (Figure 2-**1** A). The first stimulus was always at −25°, the

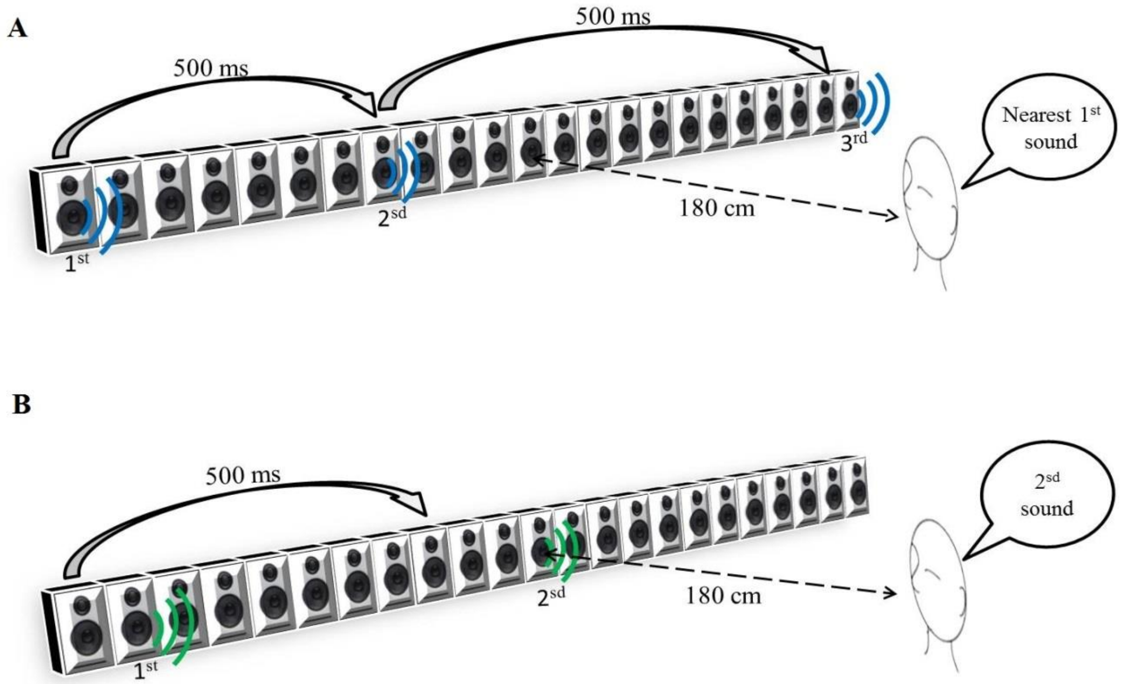


Figure 2-1. (A) Setup of the auditory space bisection. (B) Set-up of the Minimum audible angle (MAA) task.

third always at +25° and the second at an intermediate speaker position which was determined by QUEST (Watson and Pelli, 1983) , an adaptive algorithm which estimates the best stimulus value to be presented after each trial, given the current participant's estimate. To ensure that a wide range of positions was sampled, that estimate was jittered by a random amount, drawn from a Gaussian distribution of space covering the full width of the loudspeaker's array, and the nearest speaker to that estimate chosen. In the MAA task, two 75 ms pink noise (Will and Berg, 2007) stimuli were presented with a 500 ms interval. One sound came from the central loudspeaker (12th speaker) and the other one at a random distance from center on its left or on its right (Figure 2-**1** B). Also, in this case, the QUEST algorithm determined the position of the second stimulus. For both tasks, the proportion of rightward responses was calculated for each speaker distance. Gaussian functions by means of the Maximum Likelihood method were used to estimate both the accuracy and the standard deviation. The standard deviation of the fit was taken as an estimate of the threshold, indicating the precision of the task.

Results

We plotted for each participant a psychometric function of the proportion of trials judged "closer to the right sound source" against loudspeaker position (Figure 2-**2**) for each task. From each psychometric function, we calculate the point of subject equality (accuracy) and the just noticeable difference (precision). Using the precision data, we conducted a mixed model 2-way (2 × 2) ANOVA for both MAA and Space Bisection tasks with a between factor, room kind (normal room vs. anechoic chamber), and within factor, room observation (before environmental observation vs. after environmental observation). For the space bisection task the ANOVA revealed significant main effect for both factors, room observation ($F(2,22) = 6.55$, $p < 0.02$) and room kind ($F(2,22) = 7.35$, $p < 0.01$). It has been observed a significant room observation × room kind interaction ($F(4,11) = 6.86$, $p < 0.01$). Then, we ran Student's t-test that indicate a significant difference between the groups who performed the space bisection task in the normal room and anechoic chamber before observing the room (two-tailed two-sample t-test, $t(20) = 3.44$, $p < 0.01$) and in the normal room between before environmental observation and after environmental observation (two-tailed pair-sample t-test, $t(10) = 5.46$, $p < 0.001$). On the other hand, for the MAA, no significant effect was found (room observation, $F(2,22) = 0.48$, $p = 0.49$; room kind, $F(2,22) = 1.49$, $p = 0.28$; room observation × room kind $F(4,11) = 0.506$, $p = 0.481$).

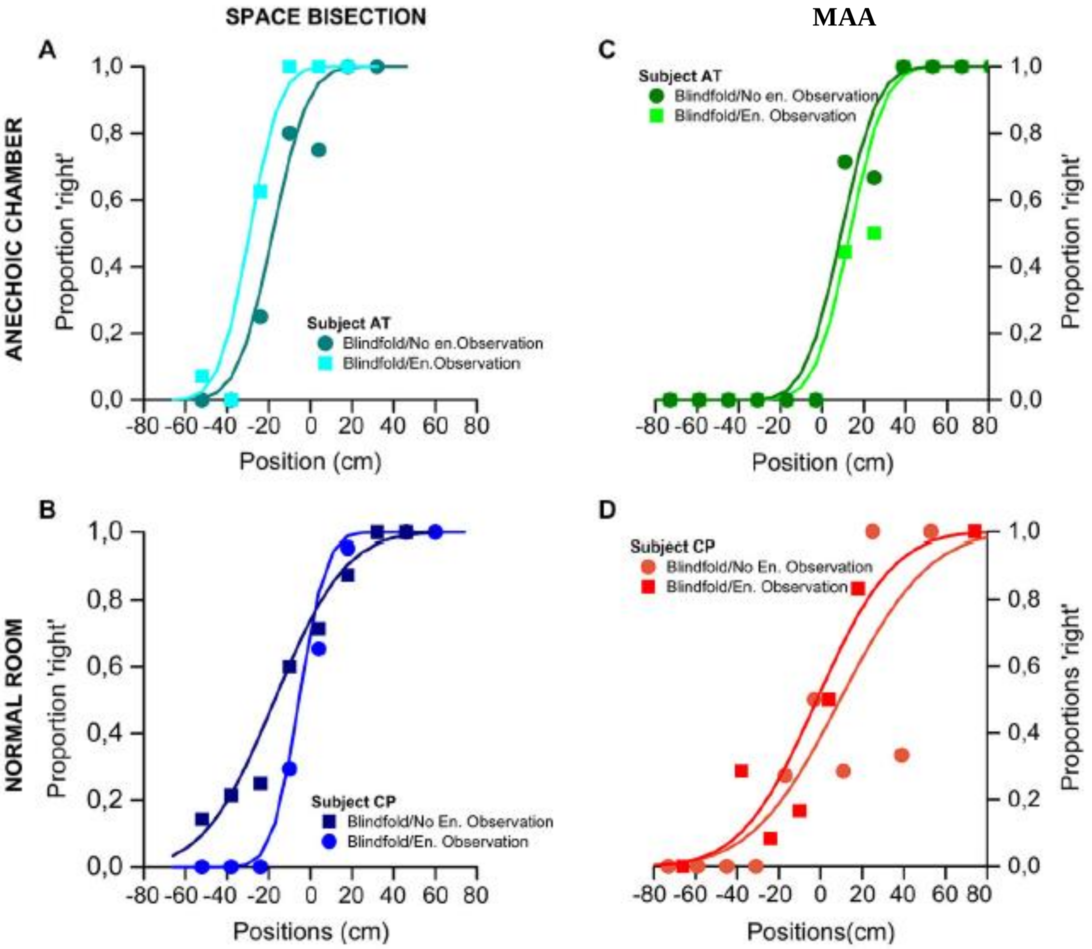


Figure 2-2. Results of the space bisection task and MAA of two representative participants, one for the anechoic chamber' group and one for the reverberant room' group. (A,B) Are the results of the space bisection of the proportion of the trials judged "closer to the third sound" plotted in function of the speaker positions (cm). On the top (A) in the anechoic chamber and on the bottom (B) for the reverberant room. (C,D) Results for the MAA as the proportion of trials where the second sound was reported to the right of the first sound plotted against different loudspeaker position. On the top (C) in the anechoic chamber and on the bottom (D) for the reverberant room.

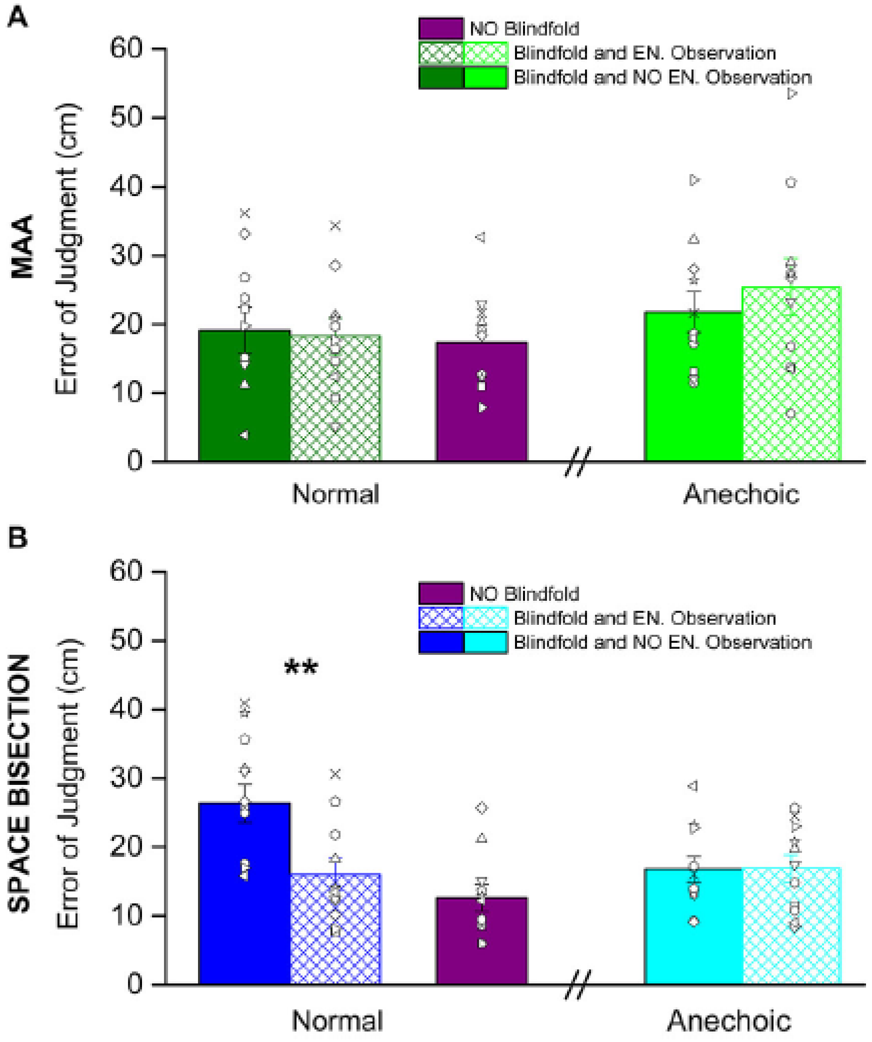


Figure 2-3. Show the average precision thresholds for the MAA and the space bisection tasks. (A) The dark green bars, on the left, represent the average precision thresholds obtained in the normal room before (fill in dark green bar) and after (reticulus dark green bar) environmental observation. On the right the light green bars are the average precision thresholds obtained in the anechoic chamber before (fill in light green bar) and after (reticulus dark light bar) environmental observation. The violet bar is the average precision obtained by the subject in full vision in the normal room. The dots represent individual data. (B) For the space bisection, dark blue bars, on the left, represent the average precision thresholds obtained in the normal room before (fill in dark blue bar) and after(reticulus dark blue bar) environmental observation. On the right the light blue bars are the average precision thresholds obtained in the anechoic chamber before (fill in light blue bar) and after (reticulus light blue bar) environmental observation. Also in this case the violet bar represent the average precision obtained by the subject in full vision in the normal room. The dots represent individual data.(**) Indicates a significant difference of precision between before and after environmental observation in the normal room($p < 0.01$).

We compared the precision “after environmental observation” and “full vision” (Figure 2-**3**) for the space bisection task (two tailed two-sample t-test, t(20) = 1.279, p = 0.27) and for the MAA (two tailed two-sample t-test, t(20) = 0.257, p = 0.799) and we found no significant difference between the two groups. No change was observed in the localization bias (PSE) for both groups and tasks (bisection task: 2-ways (2 × 2) ANOVA with factors room observation - F(2,22) = 0.79, p = 0.38, room kind, F(2,22) = 1.48, p = 0.23 and room observation × room kind interaction, F(4,11) = 0.088, p = 0.77; MAA task: 2-ways (2 × 2) ANOVA with factors room observation, F(2,22) = 0.373, p = 0.545, room kind, F(2,22) = 1.91, p = 0.175, and room observation × room kind interaction, F(4,11) = 0.001, p = 0.97).

Conclusion

In this study, we showed how visual cues help to improve precision in acoustic tasks. Importantly, the results suggest that to obtain the improvement it is not necessary to receive continuous visual inputs during the task (Tabry et al., 2013), but it is sufficient just a brief visual observation of the environment. The idea is that the just a brief observation helps to create a mental representation of the place where the task is performed that improved the degree of reliability of the metric of the environment, thanks to a calibration due to vision. This is strictly connected with the fact that the improvement is task-specific. To accomplish tasks such as the MAA, it is necessary to be able to create a relation between the position of the sound and the location of our own body, independently from the environment in which the task is performed and so the visual calibration is not needed (Lessard et al., 1998). On the contrary, in tasks like the space bisection, the knowledge of the environment plays a crucial role, inasmuch first is necessary know the location of the object (in this case sounds) in the environment, and only then it is possible to create the spatial relation between the sounds.

Another interesting result lies in the fact that the decreased performance associated with the absence of prior visual observation is evident only in a reverberant room and not in the anechoic chamber, only for the space bisection task. It might be that the null effect observed after environmental observation in the anechoic room is due to a ceiling effect, i.e., performance was best already before room observation. However, this did not happen in the reverberant room where the precision is comparable to the one in the anechoic chamber only after environmental observation, while the precision before is worse. An alternative interpretation is that the different performance in the two room in the first repetition of the task is due to the difference in the acoustic environment. In the anechoic chamber, part of the sound produced by the loudspeakers is absorbed by the walls leaving just the direct path to be absorbed by the hearing system. Differently, in the reverberant room, other than the direct path, it is present the reverberation produced by the sound reflected by the walls. The reverberation goes to add perceptual information to the direct path, generating a kind of noise generating a mismatch, which in turn decreases the precision. However, vision could help the auditory system to compensate for such mismatch and obtain performance again similar to those obtained in an anechoic chamber. The fact that only the space bisection task benefits from room observation suggest that the transfer of information from the visual system toward the auditory one occurs only when the visual system can be used to calibrate the auditory one. Increased knowledge about room acoustics through vision seems to be involved when it is necessary to estimate the complex relationship between sound sources.

To conclude, vision is important also during adulthood and not just for the development of space auditory representation in the early stages of development. In particular, vision can improve some forms of auditory spatial perception after short-term environmental observation.

2.1.2 How tactile exploration influence auditory spatial perception

In the study in paragraph 2.1.1, we demonstrated how the performance of sighted people in a auditory space bisection task can improve after a visual observation of the environment. The idea is that vision helps to create a mental representation of the environment that goes to influence the auditory cognitive maps. Along with that, several studies have demonstrated, at a perceptual level, that auditory space perception can also be biased by tactile stimuli. Similarly to the audio-visual Ventriloquist effect, auditory localization seems biased toward the side of the concurrent tactile stimulus in bimodal tasks (Bruns et al., 2011; Bruns and Röder, 2010b; Caclin et al., 2002). Specifically, tactile stimulation influences the auditory cortical activity through higher areas assigned to multimodal association (Bruns and Röder, 2010a). In this study, we investigate whether the touch is as effective as a vision to create a cognitive map of a soundscape. In particular, we tested whether the creation of a mental representation of a room, obtained through tactile exploration of a 3D model of that room, can influence the perception of a complex auditory task in sighted people, as *indirectly* vision did in the previous study. We supposed that spatial information obtained by exploring a 3D map would be poorer than that gained by visual observation. However, we wondered if, still, tactile information would be 'enough for space', meaning that essential information about the perimeter of the room, the kind of objects and their spatial relation would constitute sufficient knowledge to emulate the contribution of vision in auditory space perception (Pasqualotto et al., 2013a). We tested two groups of blindfolded sighted people – one experimental and one control group – in an auditory space bisection task. Considering the first execution as a baseline, we found an improvement in the precision after the tactile exploration of the 3D model. Interestingly, no additional gain was obtained when room observation followed the tactile exploration, suggesting that no additional gain was obtained by vision cues after spatial tactile cues were internalized. No improvement was found between the first and the second execution of the space bisection without environmental exploration in the control group, suggesting that the improvement was not due to task learning. Our results show that tactile information, as well as visual information, modulates the precision of an ongoing space auditory task. This suggests that cognitive maps elicited by touch may participate in cross-modal calibration and supra-modal representations of space that increase implicit knowledge about sound propagation.

Since, we found a variability in the benefit, due to 3D exploration, in the space bisection performance among the participants, we decided to test the mental spatial ability of participants and see whether there was a correlation with the performance in the space bisection. To do that we use to questionnaire involving mental manipulation of objects in space: the paper folding test (PFT) and the mental rotation test (MRT). The PFT requires participants to mentally perform complex spatial manipulations (Ekstrom et al., 1976) of a 2D item. Instead, the MRT evaluates the ability of mentally rotating a 3D object (Shepard and Metzler, 1971). The hypothesis was that PFT may predict an improvement obtained after the exploration of the tactile map – more similar to elicit mainly bi-dimensional representation, while the MRT would predict an improvement obtained after visual observation, which is more likely to elicit three-dimensional representations.

Participants

Twenty healthy participants (13 females, with an average age of 28.5, SD = ±7) with normal or corrected to normal vision were recruited to participate in the experiment. All participants gave informed consent in accordance with the Declaration of Helsinki before starting the tests. The study was approved by the ethics committee of the local health service (*Comitato etico, ASL 3, Genova*).

Procedure and apparatus

All participant were blindfolded before entering the room, where the experiment was performed so that during the execution of the task had no knowledge of the room nor of the setup used to produce the auditory stimuli. First, they sat in front of the loudspeakers array at a distance of 180 cm from the center and performed an auditory space bisection task (Figure 2- 4).

We divided the participants into two groups: an experimental and a control group. The experimental group, with the blindfold on, explored with both hands the 3D tactile model of the room to understand the structure of the room, the disposition of the main objects inside the room and where was located the array of loudspeakers. After that, each participant was led counterclockwise along the perimeter of the room. The participants had the chance to touch the walls and the array of loudspeakers. The participants of the experimental group then performed the space bisection a second time. Following that, the blindfold was removed for around 1 minute to allow visual observation, and the group repeated the task a third time. Instead, the control group, after the first execution of the task, had a break of 5 minutes keeping the blindfold on and then performed the space bisection a second time. Finally, the control group followed the same procedure of the experimental group for the tactile exploration of the 3D map and navigation through the environment before repeating the task a third time. Each participant performed 80 trials of the auditory space bisection per repetition, for a total of 240 trials.

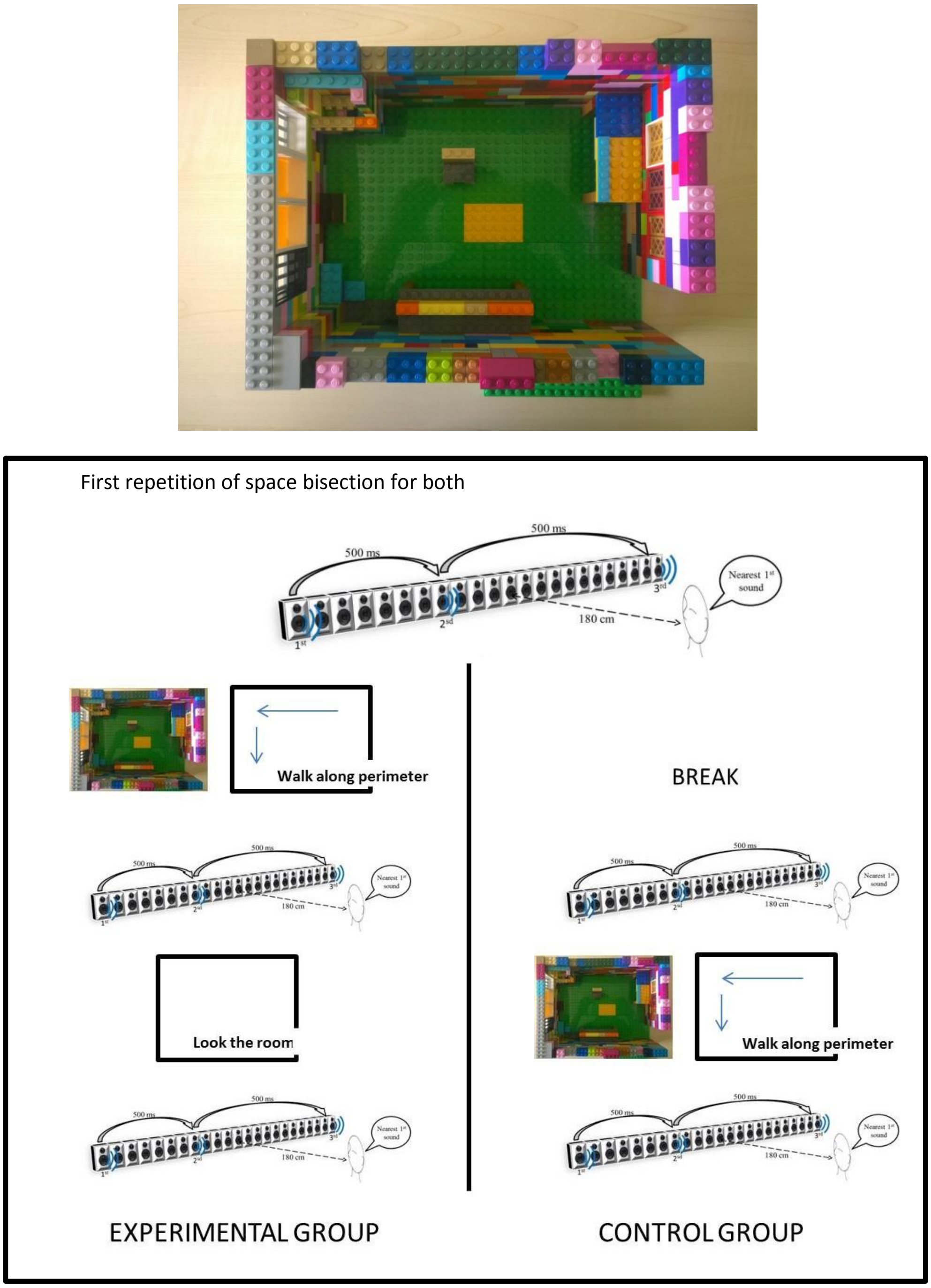


Figure 2- 4. On the top the 3D model of the room where the experiment took place seen from above. On the bottom, schema of the procedure used for the experimental group (on the left) and the control group (in the right). First, all participants performed a first repetition of the space bisection. Then participants were divided in two groups: experimental and control group, that followed a different steps.

At the end, of all participants were administered the paper folding test (PFT) and the mental rotation test (MRT) questionnaires in a random order. The PFT was administered in two parts of 10 questions each and the participants had 3 minutes to complete each part with a break of 1 minute between the parts. The time to complete the MRT was 10 minute.

The set-up for the auditory space bisection was the same described in paragraph 2.1.1. (Figure 2-1 A). Also for this experiment, the first stimulus was always at −25°, the third always at +25° and the second at an intermediate speaker position which was determined by QUEST (Watson and Pelli, 1983), an adaptive algorithm which estimates the best stimulus value to be presented after each trial, given the current participant's estimate. To ensure that a wide range of positions was sampled, that estimate was jittered by a random amount, drawn from a Gaussian distribution of space covering the full width of the loudspeaker's array, and the nearest speaker to that estimate chosen. In the MAA task, two 75 ms pink noise (Will and Berg, 2007) stimuli were presented with a 500 ms interval. One sound came from the central loudspeaker (12th speaker) and the other one at a random distance from center on its left or on its right (Figure 2-1 B). Also, in this case, the QUEST algorithm determined the position of the second stimulus. The proportion of rightward responses was calculated for each speaker distance. Gaussian functions by means of the Maximum Likelihood method were used to estimate both the accuracy and the standard deviation. The standard deviation of the fit was taken as an estimate of the threshold, indicating the precision of the task.

The room where was performed the task was 4.2 m × 3.0 m × 3.2 m (height) and the 3D reproduction of the room was made by bricks of Lego© on a scale 1:15 (Figure 2- **4**). Therefore the 3D model was represented by a 30 X 22 Lego dots matric (excluding the walls, which were two Lego dot thick), i.e. a tactile map of 27 cm X 20.7 cm. The walls of the map were 10 Lego bricks high. The bricks represented the perimeter of the room, the relevant openings (door and windows) and the main objects located in the room (two tables, the chair hosting the participant and a closet), including a representation on the array of the loudspeakers on one of the tables. A small model of a man, representing the participant, gave hint about his/her correct position and orientation inside the room. We respected the approximate relative proportions of all objects in the room. Each participant filled in two questionnaires evaluating mental manipulation ability: the PFT and an MRT. The PFT required participants to mentally perform complex spatial manipulations (Ekstrom et al., 1976). For each item on the PFT, the drawings depicted two or three folds in a square sheet of paper. The last drawing of folded paper showed a hole punched in it. Participants selected one of five drawings showing how the punched paper would look like when fully reopened. It was composed of 20 questions with scores ranging from 0 to 20, one point for each correct question. The MRT, instead,

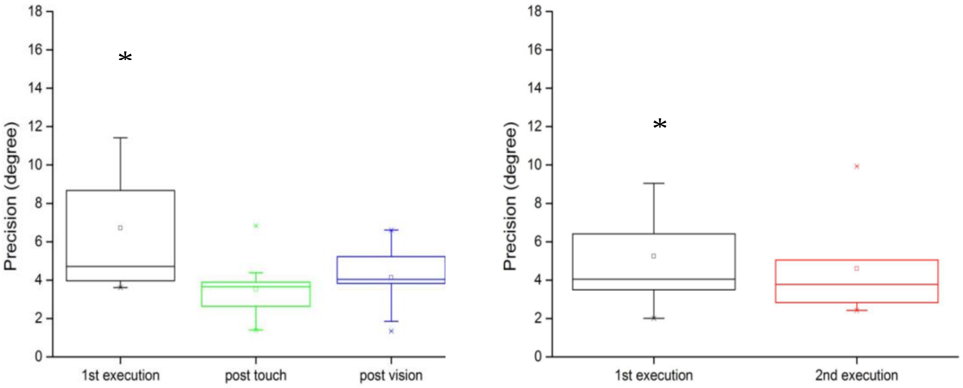


Figure 2-6. Box plot representing data of the experimental group on the left and the control group on the right.

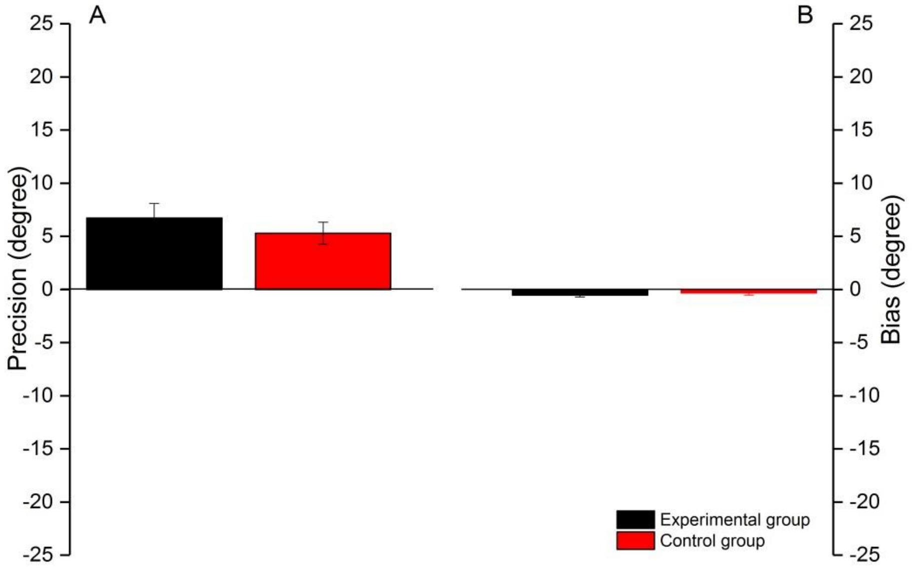


Figure 2-6. Bar plots show the precision (A) and the bias (B) in the first execution for the control group (in red) and the experimental group (in black). In the ordinate axis positive value represent the right side of the array of speakers and the negative value the left side. The 0 is the center

is composed of figures provided by Shepard and Metzler (1971), modified by Peters et al. (1995). The participants had to rotate the figures both around the horizontal and vertical axis in order to obtain the correct solution. The questionnaire is composed by 24 problems with one target figure and 4 possible responses each and in each problem set there are two and only two figures that match the target figure. The score was calculated by giving one and only one point for each correctly solved problem, i.e. both the correct matching figures are found.

Results

We checked the normality of the sample with the Lilliefors (Kolmogorov−Smirnov) test. Results showed that both the experimental and control groups were not normally distributed for the precision in the first execution of the task (experimental group, $D = 0.279$, $p < 0.03$; control group, $D = 0.277$, $p < 0.03$; for more information, Figure 2-6). The failure in respecting criteria for normality is due to the presence of two outliers performances: participant 3 in the experimental group and participant 6 in the control group. We used non-parametric statistical analysis. To see if the two samples were comparable we performed a Wilcoxon-test analysis (two-paired sample) between the first execution of the two groups. The results (Figure 2-6) revealed no significant difference between the first execution of the experimental group (black bars) and the control (red bars) for both precision ($W = 65.5$, $p = 0.26$) and bias ($W = 41.5$, $p = 0.54$), suggesting that the two groups are comparable, even if the control group is slightly more precise as compared to the experimental group. To avoid biases in the performance due to single subject variability and to calculate the effect of tactile and visual exploration, we decided to normalize the results of the post-touch and post-vision, in the experimental group, and, second execution and post-touch, in the control group, by the performance of each participant in the first execution. For both precision and accuracy (bias), we computed a relative improvement: we subtracted to each performance that obtained in the first execution, then we divided it again for the first execution. After that, we analyzed the precision in both the experimental and control groups, performing a one-sample Wilcoxon test for each condition of the experimental group, post-touch, and post-vision conditions, and control group post-touch and second execution. In the post-touch condition, we had nine participants, instead of 10. As showed in Figure 2-7, we found a significant improvement in precision for the experimental group (blue bars) in post-touch condition (filled blue bar − $V = 1$, $p < 0.01$), but not in the post-vision (lined blue bar: $V = 9$, $p = 0.06$), even if there is a trend. For the control group, we found a significant improvement for the post-touch condition (lined green bar: $V = 3$, $p < 0.02$) and not for the second execution (filled green bar: $V = 16.5$, $p = 0.28$).

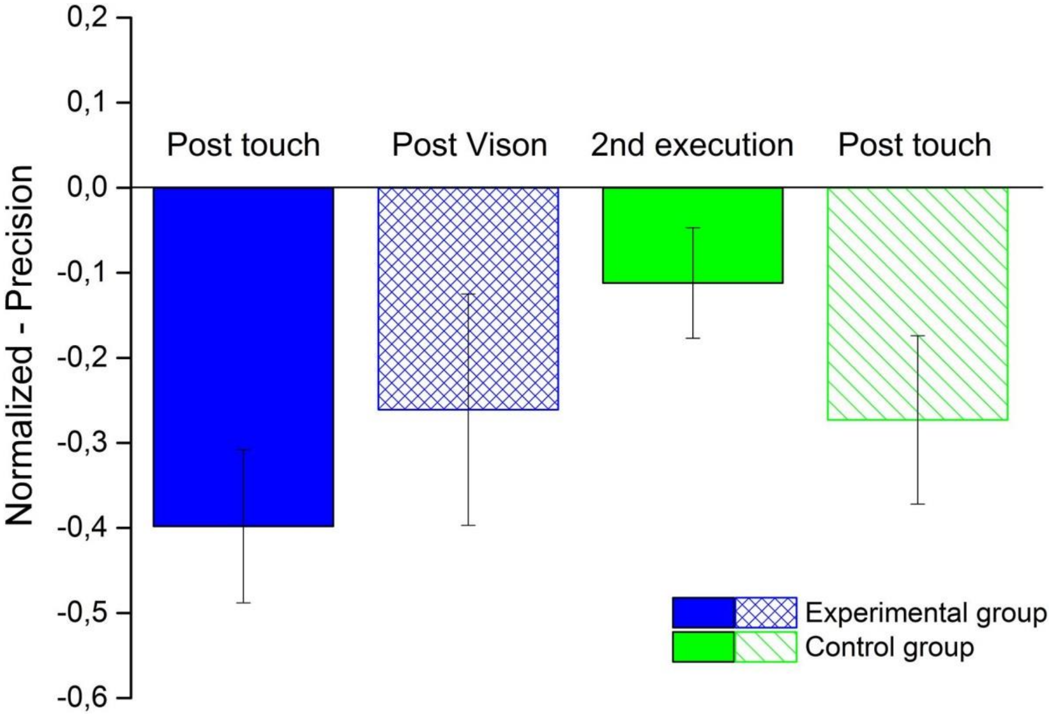


Figure 2-7 The plot represent the average precision of the experimental (in blue) and the control (in green) groups, obtained normalizing the performance of each participants by their performance in the first execution. The blue filled bar shows the post-touch condition and the lined one the post vision condition for the experimental group. For the control group the filled bar represent the second execution of the space bisection and the lined bar the post-touch condition.

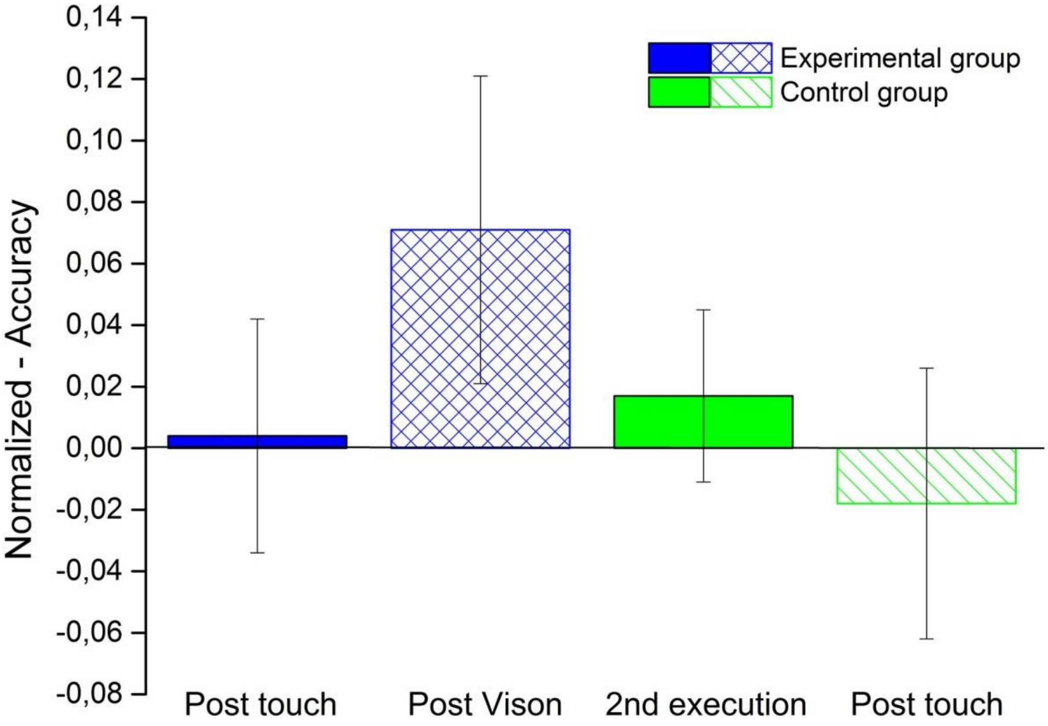
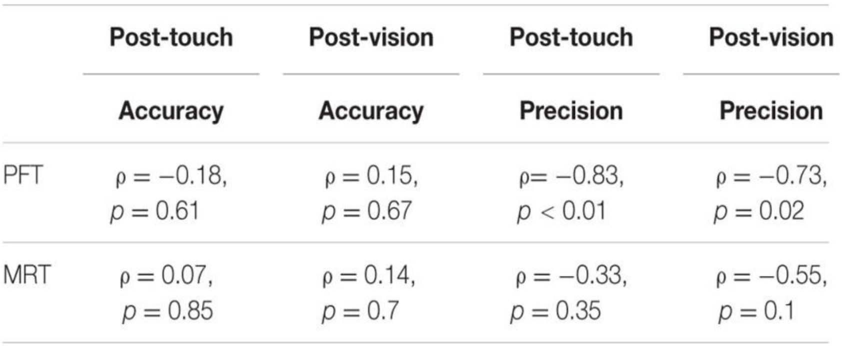


Figure 2-8. The bar plot shows the average accuracy of both groups obtains normalizing the performance of each participants by their performance in the first execution. The blue bars represent the experimental group for the condition post-touch (filled bar) and post-vision (lined bar). The green bars represent the control group for the second execution (filled bar) and the post-touch (lined bar).

On the contrary for the bias in performing the task, as showed in Figure 2-8, we did not found a significant improvement for accuracy in any condition for both control group (green bars − 2nd execution, V = 32.5, p = 0.65; post-touch V = 21, p = 0.91) and the experimental group (blue bars − post-touch, V = 27, p=1; post-vision V =39, p=0.27). Concerning the questionnaires, the average scores for the PFT were 62% of correct responses (SD = 16.5) and for the MRT was 51.7 % of correct responses (SD = 19). We computed a correlation between the percentage of correct responses in each questionnaire and the performance after tactile or visual information for both precision and accuracy. Thus, we computed a non-parametric Spearman correlation (RHO). After a Bonferroni correction for multiple comparisons, we found a negative and highly significant



	Post-touch	Post-vision	Post-touch	Post-vision
	Accuracy	Accuracy	Precision	Precision
PFT	$\rho = -0.18$, $p = 0.61$	$\rho = 0.15$, $p = 0.67$	$\rho = -0.83$, $p < 0.01$	$\rho = -0.73$, $p = 0.02$
MRT	$\rho = 0.07$, $p = 0.85$	$\rho = 0.14$, $p = 0.7$	$\rho = -0.33$, $p = 0.35$	$\rho = -0.55$, $p = 0.1$

Table 2-1. Results of the correlation between two questionnaires about spatial abilities and precision/accuracy of the auditory space bisection tasks in two conditions (post-touch and post-vision).

correlation only between the precision of post-touch condition ($\rho(20) = -0.83$, $p < 0.01$) and PFT. For the other results, see Table 2-1.

Conclusion

The present study is a continuation of what has been presented in paragraph 2.1.1. We investigated two main points: whether cognitive maps created by haptic exploration could influence precision in a complex auditory task with the same effectiveness of visual observation, and whether the skill to mentally manipulate an object could be related to the auditory space performance, after haptic or visual knowledge of the room. We found that haptic exploration, combined with vestibular feedback during navigation, increase precision in the space bisection task. The effect is not due to a learning process because the control group does not show the effect after the second repetition of the task without receiving any feedback about the structure of the room between the two repetitions. In the control group, a significant improvement was obtained after the tactile exploration of the 3D model

Previous studies, already showed that tactile information can directly influence auditory localization (Bruns et al., 2011; Bruns and Röder, 2010a; Gori et al., 2014b), the novelty of this work tactile information influence audition indirectly, thanks to the mental representation of the space create through it. One limitation of this work is that we did not counterbalance the conditions (visual and tactile) across the participants, because, otherwise, we would not have been able to assess whether the effect was due to that the mental representation, built through tactile exploration, or just vision.

Moreover, we found that there is a negative correlation between one of the questionnaire, used to evaluate mental rotation skills (Paper folding test) and the precision of the space bisection after tactile exploration, meaning that the greater is the ability to mentally manipulate a bi-dimensional object, the higher is the precision in the space bisection. A possible explanation is that it might be that the same analytic strategy used in the PFT (Kyllonen et al., 1984) could be applied also to perform the space bisection, after the recalibration from tactile exploration.

2.2 Spatial representation in visually impaired individuals

As mentioned in chapter 1, in the last few years, it is gaining more and more important the idea of a crucial influence of visual experience on the creation and calibration of spatial representations during development. As we demonstrated in the previous paragraph visual information is still important for space perception even during adulthood.

Visual experience helps to localize sounds in space and navigate through the environment given a global perception of the environment and what there is in it. The lack of visual information might lead to a self-calibration by the auditory system for space evaluation. Since the auditory system, it is less reliable compared to the visual system (Alais and Burr, 2004; Mateeff et al., 1985; Warren et al., 1981) and provides a less accurate spatial representation, the acoustic system alone cannot provide a complete spatial representation of the external world. Evidence in support of this hypothesis comes from several studies showing that early blind individuals presented impairments in some auditory task (Cappagli et al., 2015; Cappagli and Gori, 2016; Finocchietti et al., 2015; Gori et al., 2014a; Lewald, 2002; Pasqualotto et al., 2013b; Pasqualotto and Newell, 2007; Voss et al., 2015). Nonetheless, a wide literature exists where blind individuals showed an enhanced sensitivity to auditory stimuli (Gougoux et al., 2004; Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004). However, the nature and the role of this impairment remains unclear. The aim of this paragraph is to try to shed new light on auditory spatial ability in blind people.

2.2.1 Intercepting moving sounds without vision

An important aspect of our hearing is sound localization, because allow us to interact with the environment when external stimuli are not accessible with vision, but more important for people with visual impairments. The sounds present in the environment are mainly dynamic. Most of the studies investigating spatial auditory ability in visual impaired people using static stimuli (Doucet et al., 2005; Lewald, 2013; Röder et al., 1999) paired with static body position of the participant, overlooking dynamic auditory stimuli and body motion, that are more natural conditions.

The localization of visual stimuli or sound sources apparently does not change under dynamic conditions (Medendorp et al., 2002; Vliegen, 2004). For example, Vliegen (2004) found that during auditory target presentation, it is possible to compensate for ongoing saccadic eye and head movement. Perceptual stability occurs thanks to a spatial remapping of the stimulus from an egocentric (eye, head and body centered coordinates) external frame of reference that assures a stable representation of objects in world coordinates. In the acoustic domain, external stimuli are represented in both egocentric and allocentric frames of reference (Schechtman et al., 2012). Indeed, the egocentric spatial representation of sound sources that is originally deduced from the processing of binaural cues such as interaural time difference (ITD) and interaural level difference (ILD) afterward is remapped in an external frame of references, to ensure an accurate multisensory perception and sensory-motor interaction.

In the current study, we investigated the effect of early blindness on the ability to localize static and moving auditory stimuli by comparing sighted and early blind individuals' performance in different spatial tasks. We also checked perceptual stability in the two groups of participants in a static and a dynamic head condition involving rotational head movements. The hypothesis is that the lack of vision in blind participant during development might produce a deficit in remapping the space from egocentric to allocentric coordinates that usually occurs during head movements.

The results in sighted participants did not showed problem in localizing neither static nor moving sounds. Their localization ability remained unchanged after rotational movements of the head. On the contrary, blind participants showed a leftward bias during the localization of static sounds and a little bias for moving sounds. Moreover, during the localization of moving sounds blind participants with head movements showed a significant bias in the direction of the head. These results suggest that internal spatial representations might be body-centered in blind individuals and that in sighted people the availability of visual cues during early infancy may affect sensory-motor interactions.

Participants

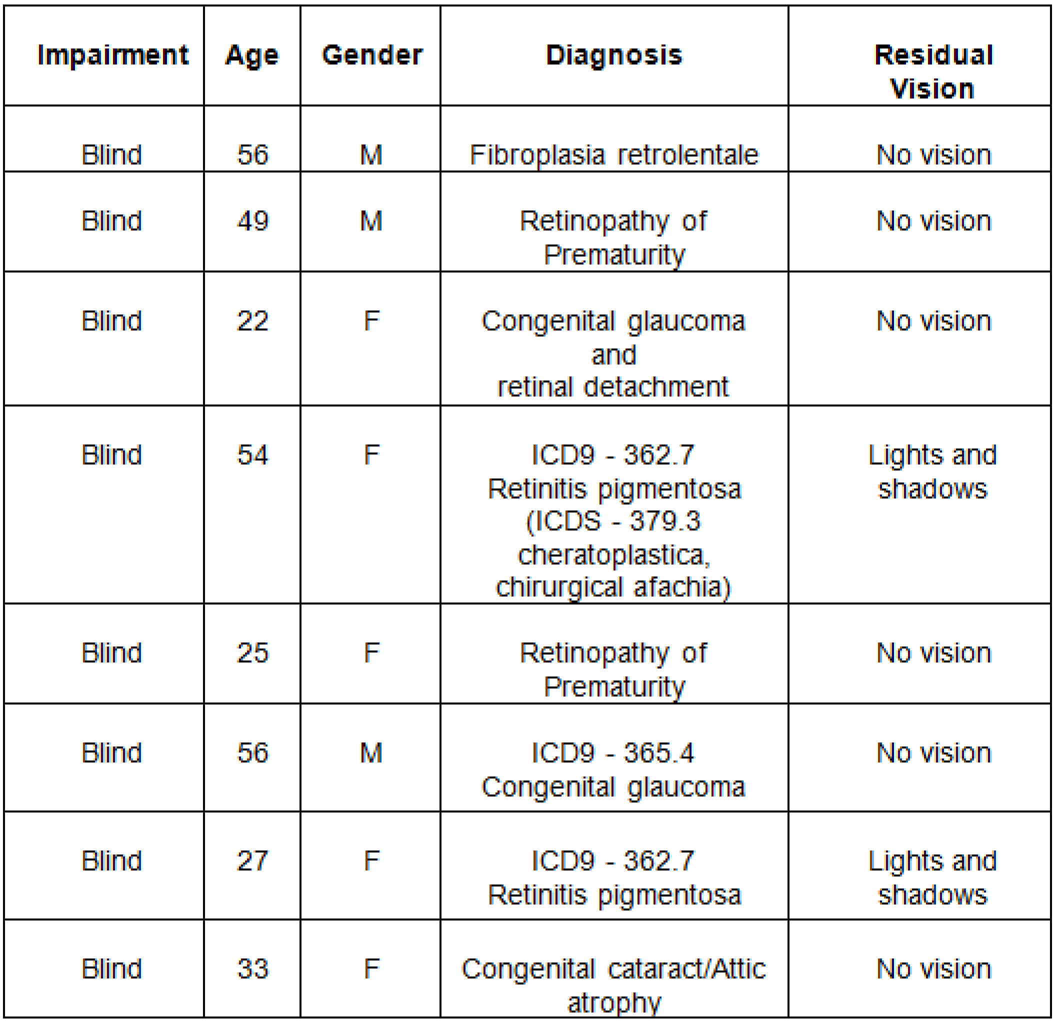
Sixteen volunteers participated in the study. Eight healthy volunteers (4 females, average age 36, SD = ± 6) and eight early blinds individuals (5 females, average age 40, SD = ± 6). Clinical details regarding the blind participants are presented in Table 2-**2**. All the EB participants were blind at birth. All the participants had no history of hearing impairment and were right-handed. The participants provided written informed consent in accordance with the Declaration of Helsinki. The study was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy).

Procedure and apparatus

Before each task, the participants were blindfolded. Each participant performed two auditory tasks: a pointing task, where the participant had to localize the source of a static sound; and a localization task with moving sounds, in which the participant had to localize the end point of the sound (**Figure**

2-9). This last task was repeated two times. In one of the repetitions, the participant had to look forward keeping the head fixed, in the other case had to perform a head movement

During the pointing task, a 300 ms sound was delivered by one of 18 speakers (**Figure 2-9** below). The experimental setup was composed of 18 speakers placed at 5 cm distance one from another and arranged in an arc with 57 cm radius. Each speaker was covered with a 4X4 array of tactile sensors, used to record participants' responses. Participants sat in the middle of the array at around 50 cm of distance. Participants had to identify and touch the speaker that produced the sound. Each participant performed a total of 180 trials, where every sound location was repeated in a random order 10 times.



Impairment	**Age**	**Gender**	**Diagnosis**	**Residual Vision**
Blind	56	M	Fibroplasia retrolentale	No vision
Blind	49	M	Retinopathy of Prematurity	No vision
Blind	22	F	Congenital glaucoma and retinal detachment	No vision
Blind	54	F	ICD9 - 362.7 Retinitis pigmentosa (ICDS - 379.3 cheratoplastica, chirurgical afachia)	Lights and shadows
Blind	25	F	Retinopathy of Prematurity	No vision
Blind	56	M	ICD9 - 365.4 Congenital glaucoma	No vision
Blind	27	F	ICD9 - 362.7 Retinitis pigmentosa	Lights and shadows
Blind	33	F	Congenital cataract/Attic atrophy	No vision

Table 2-2. Clinical details of early blind participants. The table shows the age at the time of the test, gender, pathology and residual vision at the time of the test

In the localization task with moving sounds, participants first had to keep their head straight while listening to a moving sound, from left to right or from right to left. Instead, the duration of the

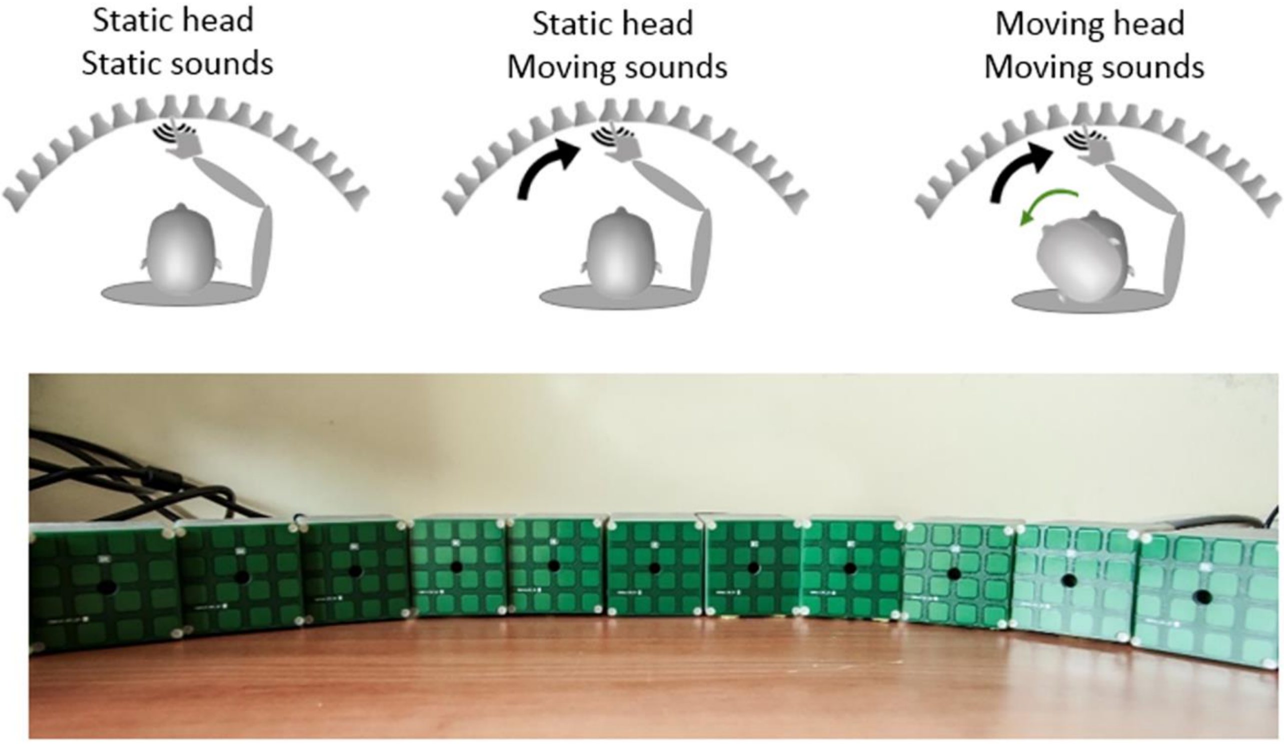
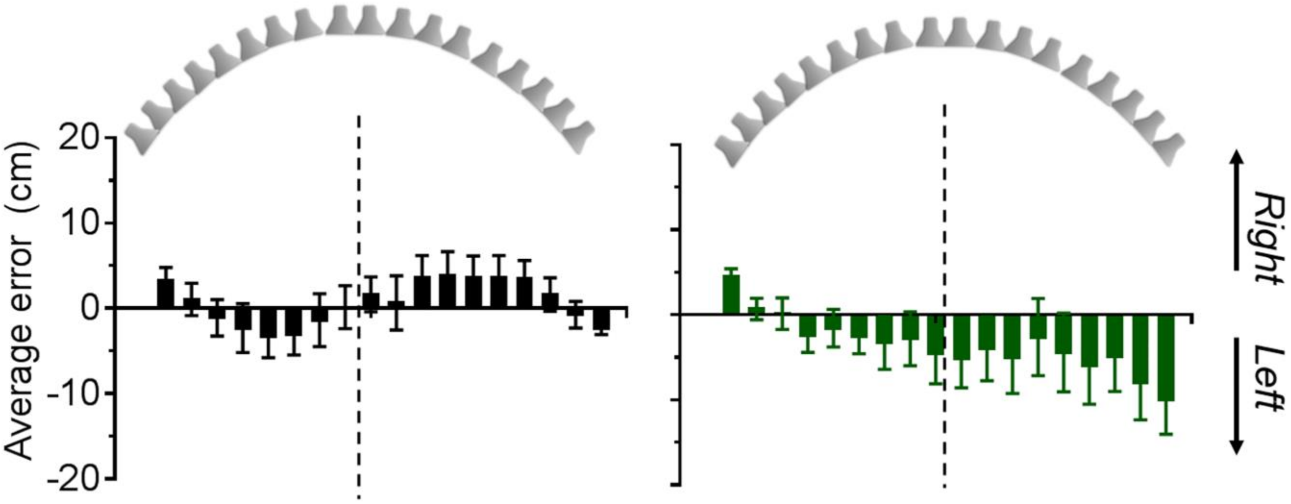


Figure 2-9. Set-up of the experiment. The upper part shows the procedure for the three different localization tasks. The lower part shows a picture of the experimental set-up.

moving sound was manipulated across three values: 200, 300 and 500 ms, consequently it was also manipulated the velocity of the sound. After the presentation of the moving sound, participants had to locate its endpoint by touching the last speaker that produced a sound. We modified the direction of the sound generating a “rightward” and a “leftward” condition. For each direction of the moving sound, participants performed three experimental blocks, one for each stimulus duration. The endpoint of the moving sound ranged from one of this location: -7.5, 2.5,12.5,22.5 and 32.5 cm in the rightward condition. The endpoints in the leftward condition were -32.5, -22.5, -12.5, -2.5 and 7.5.

The negative values represent the left side and the positive values the right side array. Each endpoint location was repeated 10 times in a constant stimuli algorithm in a random order, for a total of 100 trials. In the localization task with head movement, we used the same auditory stimuli, but this time participants had to perform a head rotation during the sound presentation. We asked participants to rotate the head in the opposite direction of the sound (for example they had to move the head to the right side, while the sound was moving from right to left, in the leftward condition). The movement of the head started after a go signal, that was synchronized with the start of the sound. At the end of the auditory stimulus, participants had to maintain the head rotated and localize the endpoint of the moving sound by touching the speaker with their right hand. Also, in this case,



participants performed a total of 100 trials for each time duration block. Before the experiment, we trained participants to perform a precise head movement.

Auditory stimuli were static or moving sounds (white noise burst), presented at 70 dB of sound pressure level. We recorded motor responses by using tactile sensors directly attached to the speaker surface and head movements by using the Vicon motion tracking system (Vicon Motion Systems, Ltd., UK). This is an infrared marker-tracking system that acquires live movements in 3D space with high temporal and spatial precision. For an accurate analysis, we used seven markers: three of them were placed on participants' shoulders to form a horizontal line, two markers were placed above the ears, one on the forehead and one above the inion. These last two markers generated a vertical line on the antero-posterior axes of the brain. We measured the intersection between the horizontal and the vertical line and calculated the amplitude of the angle produced by the rotation of the head and the speed of the head movement.

Figure 2-10. Average errors for each loudspeaker location (that are represented by the grey loudspeakers) for sighted (plot on the left in black) and blind (plot on the right in green) participants measured in the localization task with static sounds.

Results

For the pointing task with static sounds, first, we calculated the average errors for each participant as the difference between the reproduced and the correct location of the sound and then averaged across participants for each group. The results are plotted in Figure 2-10 for each speaker location. Negative values represent a misallocation to the left, while positive value on the right. The dashed line represents the central position of the speaker's array so that bars on the right side of the line stand for loudspeakers on the left side of the array. We run a repeated measured ANOVA with between factor group (blind and sighted) and within factor sound positions. It was found a significant main effect for sound position ($F_{(2,16)} = 2.95$, $p < 0.001$, $\eta 2 = 0.71$) and a significant interaction between sound position and group ($F_{(2,17)} = 2.89$, $p < 0.001$, $\eta 2 = 0.17$). We found a small tendency in the group of sighted to expand the auditory space, i.e. there is a displacement of the location of the sound on the right side of the array to the right (positive errors) and location on the left side of the array to the left (negative errors). However, errors were not statistically different from zero. On the other side, the group of early blind participants shows a significant bias to the left (one sample two-tailed t-test: $t_{17} = -4.53$, $p < 0.001$). A repeated measure ANOVA revealed a significant effect of the speaker location ($F_{17} = 4.43$, $p<0.0001$, $\eta 2 = 0.38$). Specifically, the error in localizing the last speaker on the right was significantly higher than all the others (all $p<0.01$).

For the localization task with fixed head and moving sound, we run a repeated measure ANOVA with within factors: motion direction, speed and endpoint location and between factor group. For this task, the errors were calculated as the difference between reproduced endpoint locations measured in the localization task with fixed head and reproduced locations measured in the pointing task. Moreover, we normalized errors to correct for the direction of motion so that positive values of the error represent a bias in the direction of the motion. Since endpoint locations were specular for the two motion direction conditions, we considered 5 endpoint locations from 1 (most central) to 5 (most peripheral). We found a significant interaction between endpoint location and group ($F_{(2,4)} = 4.11$, $p = 0.006$, $\eta 2 = 0.25$), but no effect of speed and motion direction. The results are shown in Figure 2-**11** for sighted (black symbols and line) and blind (green symbols and line) participants. As we did not find any significant effect of speed, we averaged individual data across the three-speed conditions. Group means errors are plotted as a function of all the endpoint locations of the sound. A positive value of the error represents a displacement toward the direction of sound motion. On average error were significantly different from zero (showing a bias in the direction of sound motion) only for blind participants when the sound ended 5 cm to the right (one sample, 2-tailed t-tests with Bonferroni

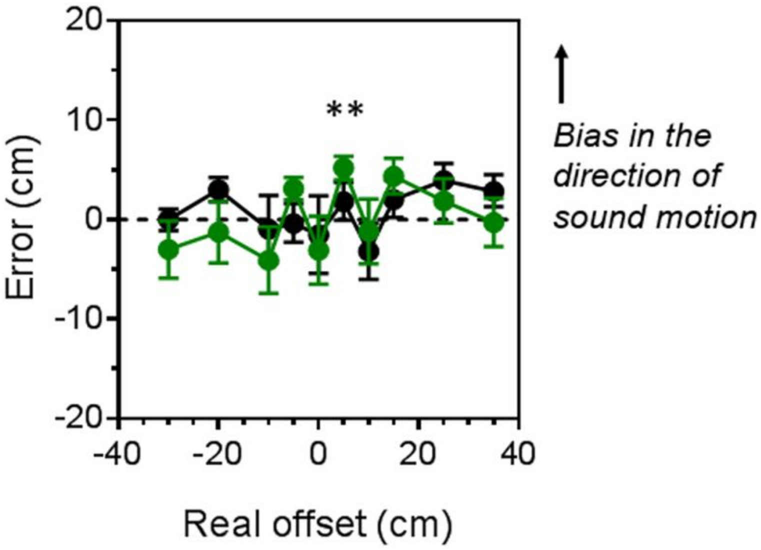


Figure 2-11. Average errors measured in the localization task with moving sounds and static head for blind (in green) and sighted (in black) participants calculated based on the bias find in the localization task with static sounds. Data in this picture are averaged across the three speed conditions (200, 300 and 500 ms) since we did not find any significant difference.

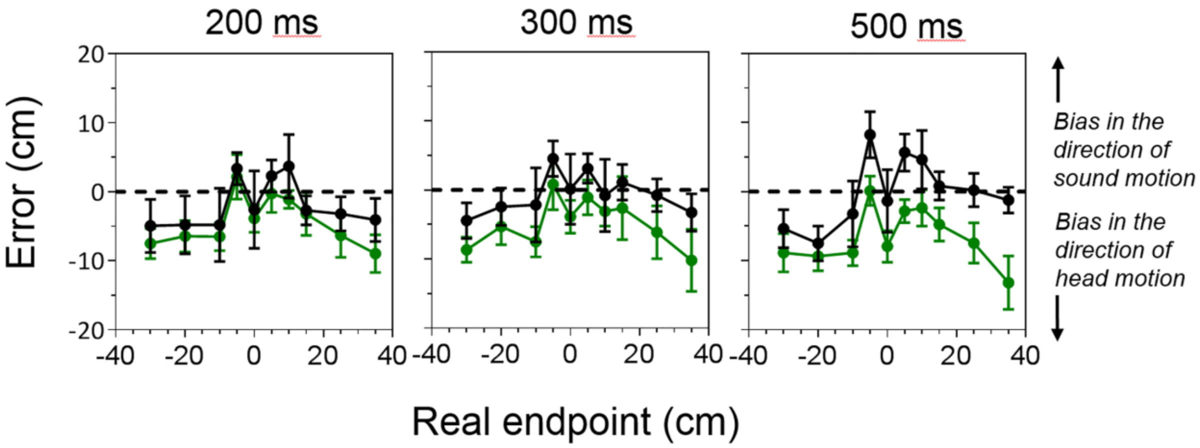


Figure 2-12. Average errors measured in the localization task with moving sounds and moving head for blind (in green) and sighted participants, calculated based on the bias find in the localization task with static sounds. Data in this picture are averaged across the three speed conditions (200, 300 and 500 ms) since we did not find any significant difference.

correction for multiple comparisons, $t_7 = 4.73$, $p = 0.002$). Sighted controls' error, when the sound ended 25 cm to the right, was only marginally significant (one sample, 2-tailed t-tests with Bonferroni correction for multiple comparisons, $t_7 = 2.44$, $p = 0.04$).

The head rotation differently affected the performance of the two group of participants, with blind individuals showing a bias in the direction of head motion. Results for the localization tasks with moving sounds and moving head are reported in Figure 2-**12**. Group means errors are calculated as for the task performed with a fixed head. Errors were normalized to correct for the direction of motion so that positive values of the error represent a bias in the direction of sound motion and negative values of the error show a bias in the direction of head motion. A repeated measure ANOVA (within factors: motion direction, speed and endpoint location; between factor: group) showed a significant interaction between motion direction, endpoint location and group ($F_{2,4} = 4.12$, $p = 0.008$, $\eta 2 = 0.31$); motion direction and endpoint location ($F_{2,4} = 8.9$, $p<0.001$, $\eta 2 = 0.49$); speed and endpoint location ($F_{2,4} = 3.28$, $p = 0.003$, $\eta 2 = 0.26$); endpoint and group ($F_{2,4} = 3.42$, $p = 0.01$,

$\eta 2 = 0.27$); and a significant effect of endpoint location ($F_{2,4} = 13.72$, $p<0.001$, $\eta 2 = 0.6$). Pairwise comparison (corrected for multiple comparisons) revealed that the mislocalization of peripheral speakers was larger than the mislocalization of the most central speakers ($p<0.002$).

For the rightward condition, differences in localization's error between the two groups of participants were significant only for the 500 ms condition (repeated measure ANOVA, group for the 500 ms condition; within factors: endpoint location; between factor: group, $F_{(4,1)} = 9.28$, $p = 0.009$, $\eta 2 = 0.39$). We also compared localization error measured in this task with localization errors observed in the task with moving sound and static head. A repeated measure ANOVA (within factor: head, speed and endpoint; between factor: group) showed a significant effect of head ($F_{3,4}$ = 8.44, p = 0.01, η2 = 0.37) and endpoint ($F_{3,4}$ = 6.57, p< 0.001, η2 = 0.44), a significant interaction between head and group ($F_{3,4}$ = 4.66, p = 0.04, η2 = 0.25) and head and endpoint ($F_{3,4}$ = 15.09, p<0.001, η2 = 0.40). Similarly to the rightward condition, for the leftward condition, a repeated measure ANOVA (within factor: head, speed and endpoint; between factor: group) showed a significant interaction between endpoint and group ($F_{3,4}$ = 3.88, p = 0.01, η2 = 0.30) and head, endpoint and group ($F_{3,4}$ = 3.49, p = 0.01, η2 = 0.28).

Conclusion

Two main results are evident from this study. First results of this study are that early blind people are influenced by rotational head movements during auditory localization of moving sounds, while sighted people are not. The bias found in blind people is in the same direction of the head movements, i.e. when they have to move the head on the right while the sound is going in the opposite direction they will tend to shift the end point of the moving sound to the right, and vice-versa. This result suggests that early visual deprivation influences the spatial representation because in the head movement condition there is not a modification according to the requirement of the task to be performed for blind individuals. Blind individuals are less able to remap the space from an egocentric to an allocentric frame of reference, make them more susceptible to a motor bias. This is due to the fact that vision is the most accurate sense to define spatial information thanks to a simultaneous proximal and distal representation. The reduction of distal information and the lack of external landmarks (beyond the reachable space) in early blinds may prompt the use of an egocentric frame of reference because the allocentric one becomes more difficult to process (Finocchietti et al., 2017; Gori et al., 2014a).

A second result is that the early blind group show a displacement of static sounds toward the left side of space, in contrast with previous literature (Lessard et al., 1998; Röder et al., 1999; Voss et al., 2015). This bias may be appointed to the spatial resolution provided by our setup allowed us to highlight small spatial errors that otherwise might not be detectable (loudspeaker distance = 5 cm). In previous the distance between speaker was 10 cm, that is the largest error reported in this task.

2.2.2 Body-centered or external reference frame? How congenitally blind individuals localize sounds

As mentioned in chapter 1, there are several studies showing that blind individuals have task specific auditory spatial impairments (Cappagli and Gori, 2016; Gori et al., 2014a; Vercillo et al., 2016; Voss et al., 2015). For example Finocchietti et al (2015) found that ability of early blind individuals to encode the trajectory of a 2-dimensional sound motion, reproducing the complete movement, and reaching the correct end-point sound position is impaired, showing a clear deficit in encoding the sound motion in the lower side of the plane testes. This impairment is not present in late blind and sighted people. However, the nature and the role of the impaired auditory spatial processing remains unclear, even because it is present just for some kind of tasks.

One hypothesis is that the task-specific differences in auditory spatial processing might be related to the use of body-centered and external frames od reference by blind individuals. At the begin sounds are represented in head and ear-centered frames of reference to ensure a spatial alignment between auditory and visual stimuli (Cohen & Andersen, 2002; Jay & Sparks, 1987)., and just with a second passage this representation is transformed. Afterward, the positions of auditory stimuli are linked to external objects (external frames of references), supporting integration across all the sensory modalities, guaranteeing perceptual constancy despite body movements, and facilitating sensory-motor interaction. External frames of reference provide spatial information for the coordinated movement of multiple effectors and for this reason, are crucial to guide actions (Cohen & Andersen, 2002). Without vision and the external landmarks acquired through it, the spatial remapping into world-centered frame id reference may not occur, especially of audition (Röder, Kusmierek, Spence, & Schicke, 2007, Röder,Rösler, & Spence, 2004)).

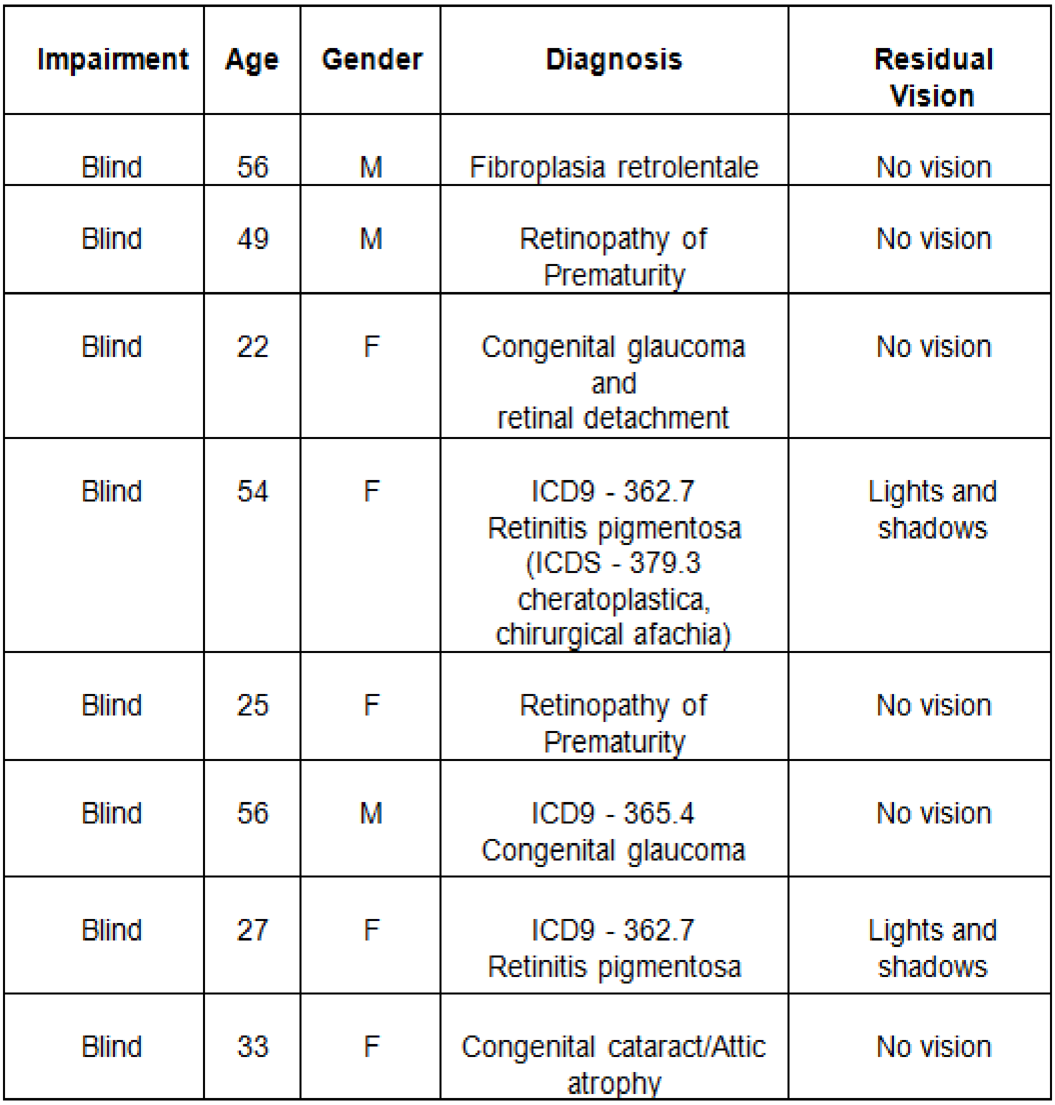
If the contribution of vision is crucial for spatial remapping of sounds in external coordinates, we should be present a deficit for localization od sounds in external frames of reference in the early blind population, but not during localization of sounds sources respect to the body.

The purpose of this study was to test this hypothesis. We developed four auditory tasks: two to evaluate the use of body-centered reference frame, and two to evaluate the use of an external frame of reference.

We found that blinds performance was severely impaired when they were required to localize auditory stimuli using external acoustic landmarks (external reference frame) or when they had to reproduce the spatial distance between two sounds. The impairment was not found in sighted participants. However, blinds performed similarly to sighted controls when had to localize sounds with respect to their own hand (body-centered reference frame) or to judge the distances of sounds from their finger. These results suggest that early visual deprivation and the lack of visual contextual cues during the critical period induce a preference for body-centered over external spatial auditory representations.

Participants

Took part to this study eighth early blind (5 females, average age 40.12, SD = 6 years of age) and ten sighted individuals (5 females, average age: 34.7, SD = 6 years of age). There was not a significant difference in age between the two groups of participants (2-tailed independent sample t-test, $t_{15} = -1.16$, $p = 0.26$). Additional information about blind participants is reported in Table 2-3. All participants signed written informed consents in accordance with the Declaration of Helsinki. For blind participants, the form was read by the experimenter. The study was approved by the ethical committee of the local health service (Comitato etico, ASL 3 Genovese, Italy).



Impairment	Age	Gender	Diagnosis	Residual Vision
Blind	56	M	Fibroplasia retrolentale	No vision
Blind	49	M	Retinopathy of Prematurity	No vision
Blind	22	F	Congenital glaucoma and retinal detachment	No vision
Blind	54	F	ICD9 - 362.7 Retinitis pigmentosa (ICDS - 379.3 cheratoplastica, chirurgical afachia)	Lights and shadows
Blind	25	F	Retinopathy of Prematurity	No vision
Blind	56	M	ICD9 - 365.4 Congenital glaucoma	No vision
Blind	27	F	ICD9 - 362.7 Retinitis pigmentosa	Lights and shadows
Blind	33	F	Congenital cataract/Attic atrophy	No vision

Table 2-3. Clinical details of early blind participants. The table shows the age at the time of the test, gender, pathology and residual vision at the time of the test.

Procedure and apparatus

All participants performed four auditory tasks to evaluate the use of frames of reference (external or body-centered): two kind of space bisection and two distance reproduction tasks Figure 2-**13**. Before starting the experiment, to blind people were allowed to explore the setup tactually, and to sighted people visually. During all tasks, sighted people were blindfolded.

In the external space bisection task (Figure 2-**13** A), the participants heard three consecutive sounds. Sounds were always presented from left to right. We referred to the second sound of the sequence as the reference stimulus. Participants were asked to verbally report whether the reference stimulus was closer to the first of the third sound. This condition requires locating the reference stimulus using an external frame of reference because it is necessary to put in correlation the different locations of the sounds between them. The position of the reference stimulus was balance across two spatial locations: ± 7.5 cm from the center of the array of speakers. The position of the first and third sound varied at each trial. Specifically, one was delivered at ± 20 cm from the reference and

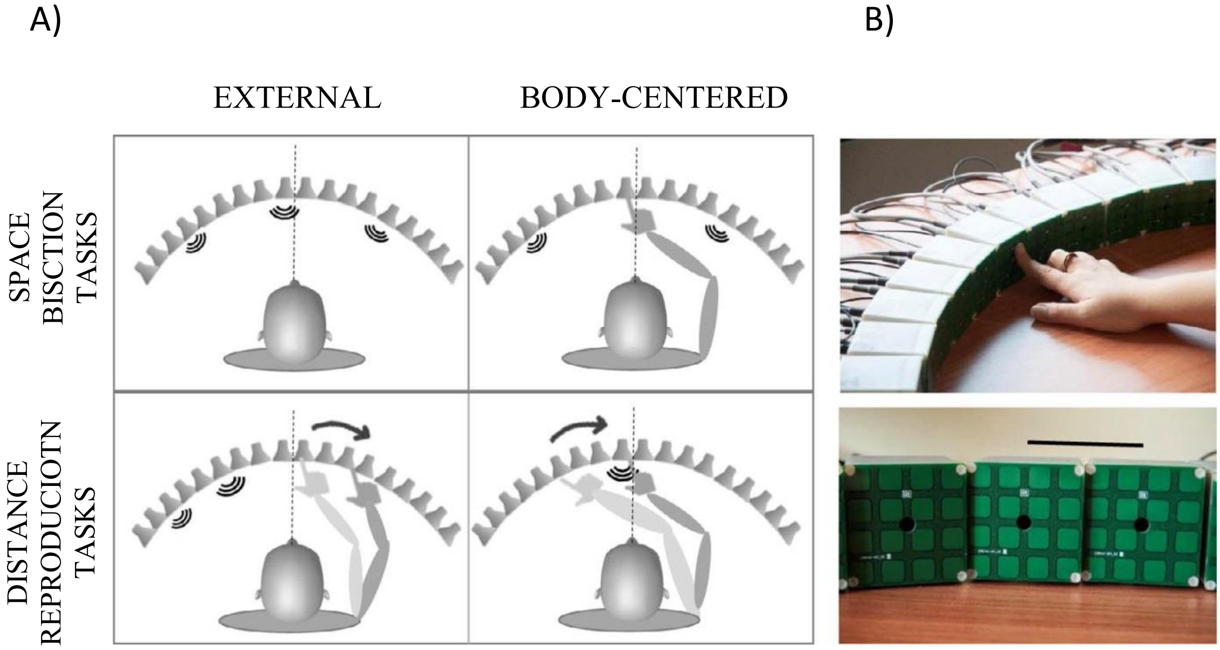


Figure 2-13. (A) The upper two figures show the experimental procedure for the space bisection tasks. In the external reference frame condition (on the left) were presented three consecutive sounds and participants had to report whether the second sound was closer to the first or the third. In the body-centered condition (on the right), participant's hand was placed on a specific loudspeaker and a sequence of two sounds was presented, one always on the right and one on the left of the hand. Participants had to report whether their hand was closer to the first or the second sound. The lower two figures show the distance reproduction tasks. In the external reference frame condition, participant's finger was placed on the central loudspeaker (arm in light gray) and were presented two sounds in sequence on the left side of the set-up. Participants reproduced the distance between the two sounds using their finger (dark grey arm shows the final position). In the body-centered condition, participant's finger was placed in a loudspeaker (arm in light gray) and a sound was presented on the right side of the set-up. Participants reproduced the distance between their finger and the sound using their finger (dark grey arm). (B) Picture of the speaker using during the experiment

the other one at a distance decided by a constant stimulus algorithm, ranging between ±5 and ±35 cm (at step of ±5 cm), where positive values represent a position to the right and negative value a position to the left side of the participant. Each distance value was repeated 20 times, 10 from each reference position. In the 50% of the trials, the first stimulus was delivered at ± 20 cm. Each participant performed a total of 140 trials.

In the body-centered space bisection task (Figure 2-**13** A), at the beginning of each trial, the participant index finger was placed on a speaker. The position of the speaker was balanced across two spatial locations: ± 7.5 cm from the center of the array of speakers. In this task, the reference is represented by the index finger of the participant. Afterward, we presented a sequence of two sounds, from left to right. Participants reported whether their finger (the reference) was closer to the first or the second sound. This condition does not require the use of external reference frame, but rather a body-centered spatial representation. The two sounds were presented one at ± 20 cm from the reference and the other one at a distance decided by a constant stimulus algorithm, ranging between ±5 and ±35 cm (at step of ±5 cm), where positive values represent a position on the right and negative value a position on the left side of the participant. The number of trials and repetition for each position of the sound and the index finger was the same of the external space bisection.

In the external distance reproduction task (Figure 2-**13** A), at each trial, the experimenter placed the index finger of the participant on a speaker at the + 2 cm position from the center of the array of the loudspeakers. Afterward, two sounds were presented in the sequence (from left to right). The participants had to estimate the distance between the two sounds and reproduce that distance using their right index finger. They used their finger as a starting point and moving it to reproduce the distance. The first sound was always located at -42.5 cm or at -27.5 cm. the second sound could be presented at variable distances from the first sound in a range between +5 and +25 cm (at the step of 5 cm). Each participant completed a total of 100 trials, each distance was repeated 10 times for each finger's position.

In the body-centered distance reproduction task (Figure 2-**13** A), before starting each trial the index finger of each participant was placed on one of two loudspeakers located at -42.5 cm or -27.5 cm from the center of the array. After, a sound was presented at a variable distance from the finger, in a range between +5 and +25 cm (at the step of 5 cm). The task was to estimate the distance between the finger and the sound, by reproducing the distance moving the finger to the right of the starting position. Participants performed a total of 100 trials, each distance was repeated 10 times for each finger's position.

For each task, it was used an array of 18 loudspeakers with a shape of an arc so that each speaker was at the same distance from the head of the participant. The array was positioned on a table at 57 cm from the participant so that each speaker was easily reachable with the index finger. We used a 300 ms white noise burst as auditory stimulus at 70 dB of sound pressure level. To record the motor responses, we used tactile sensors directly attached to the speaker surface (Figure 2-**13** B). Methods and procedures were modified adapted for our purpose from Schenk (2006), Thaler & Goodale (2011), and Gori (2014a). In none of the four task, the inter trail interval was fixed. the experimenter started each trial after recording the response of the participant. During each task, the experimenter sat in front of the participant on the other side of the table to monitor that the participants at the beginning of each trial was looking in front of them and to place their finger on the proper loudspeaker.

Results

For the external space bisection, we considered correct the proportion of trials where the reference stimulus was judged “closer to the third sound”. Instead of the body-centered space bisection, the proportion of right trials was calculated considered when the finger (reference stimulus) was judged “closer to the second sound”. For both tasks, we calculated the spatial relationship between the reference stimulus with respect to the two external sounds for each trial. We calculated the difference between the distance of the reference stimulus from the first sound (D1) and from the

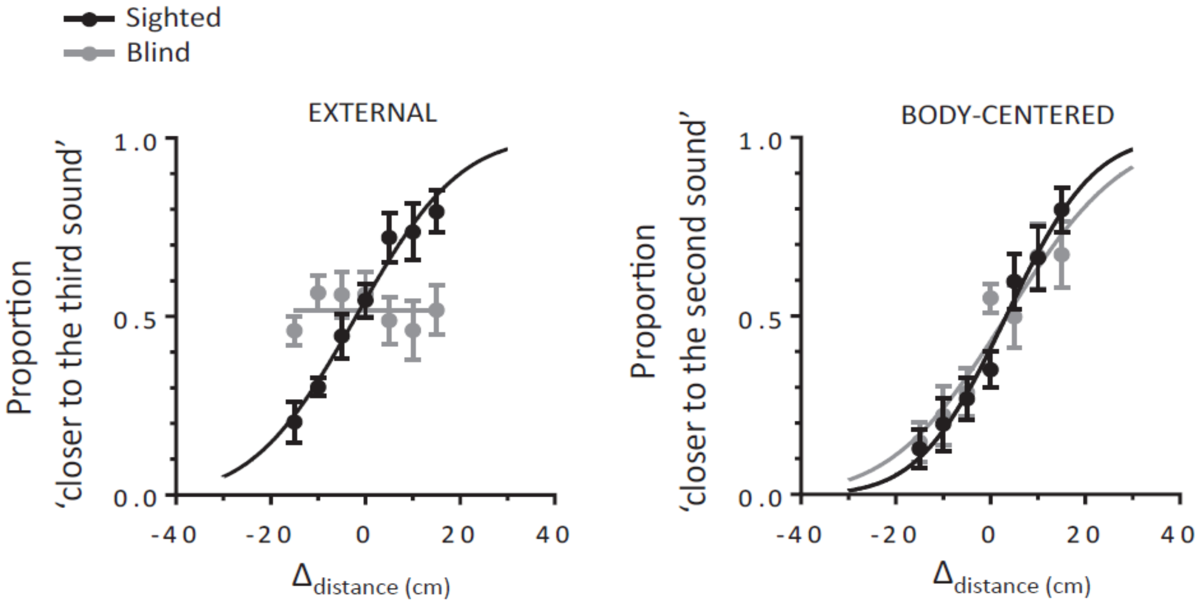
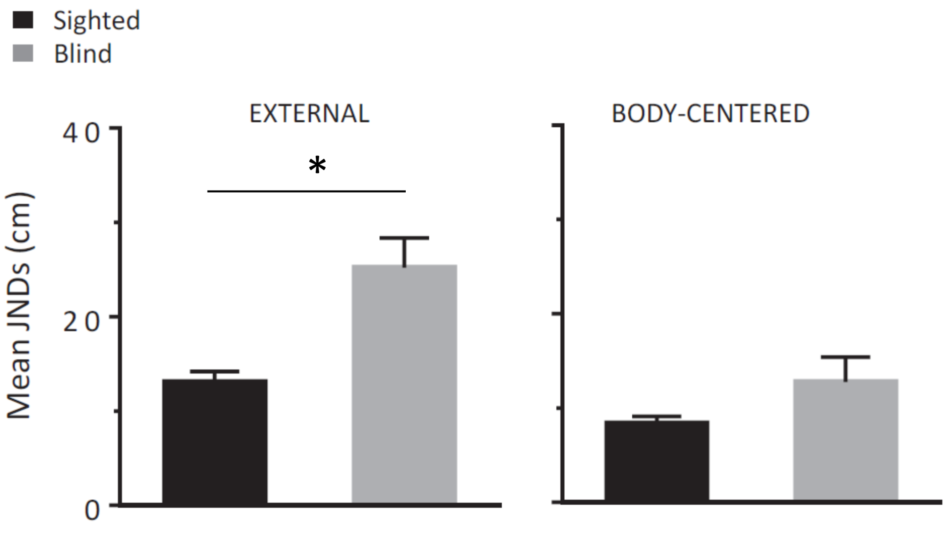


Figure 2-14. Average psychometric functions for the external (on the left) and body-centered (on the right) perceptual tasks for sighted (black curves) and blind (grey curves) participants. The curves represent the proportion of “closer to the third sound” - external condition - or “closer to the second sound” –body-centered condition – as a function of the $\Delta_{distance}$.

other sound (D2). We subtracted the two distances to obtain the $\Delta_{distance}$. A positive value of the $\Delta_{distance}$ means that the reference stimulus was closer to the last sound, on the contrary, negative value located the reference stimulus closer to the first sound. The psychometric functions, for both tasks, was calculated using Gaussian functions by means of the Maximum Likelihood method and were used to estimate both the accuracy and the standard deviation. The standard deviation of the fit was taken as an estimate of the threshold, indicating the precision of the task. For the analysis we took into account the precision in performing the tasks, obtain by the slop of the psychometric function, that indicate the minimum spatial displacement perceived by the participants. The results for the two space bisection tasks are shown in Figure 2-**14**. We reported the average psychometric functions for the sighted (in black) and the blind (in grey) participants. We run a repeated measure 2-way ANOVA with within factor Frame Of Reference (body-centered vs external) and between factor Group (blind vs sighted). We found a main effect for both factors: Frame Of Reference ($F_{(1,1)} = 27.8$, $p < 0.001$) and between factor Group ($F_{(1,1)} = 16.3$, $p = 0.001$); and a significant interaction between the factors ($F_{(1,1)} = 5.5$, $p = 0.03$). A post-hoc analysis with Bonferroni correction for multiple comparisons showed a significant difference between the precision of sighted and blind participants in performing the task only in the external frame of reference task (two-tailed unpaired t-test, $t = -4.19$, $p = 0.001$). Average precision for the sighted participants in the external condition was 13 ± 3 cm, instead of for early blind participants was 25.2 ± 3cm, almost the double compared to sighted people (Figure 2-**15**).

For the distance reproduction tasks, we measured the reproduced distances for each trial. Average results are shown in Figure 2-**16**. We run a repeated measure 3-way ANOVA with within factor Frame Of Reference (body-centered vs external) and Real Distance and between factor Group

Figure 2-15. Mean of precisions in the space bisection tasks for blind (grey bars) and sighted (black bars) participants.



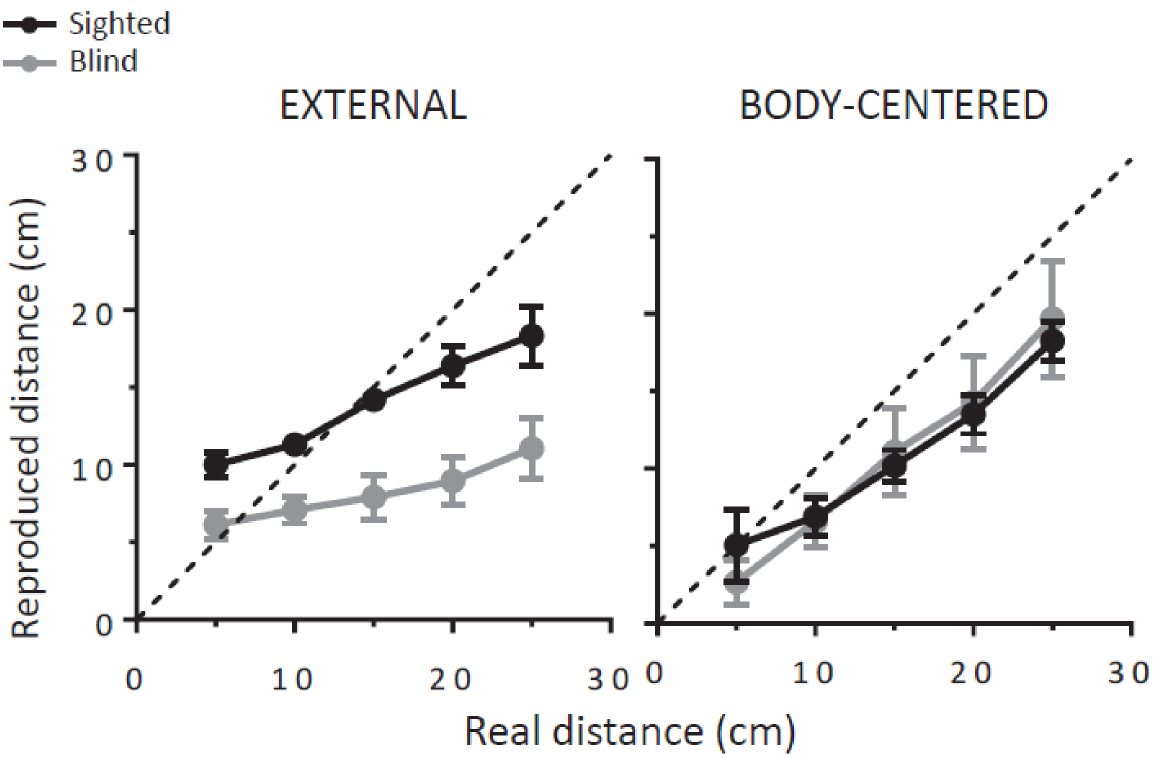


Figure 2-16. Average distances reproduced from sighted (in black) and blind (in grey) participants in the distance reproduction tasks plotted as a function of the real distance between the two sounds in the external reference frame task and between the sound and participant’ finger in the body-centered task.

(blind vs sighted). We found a main effect for Real Distance ($F_{(1,4,1)} = 62.13$, $p < 0.001$) and significant interactions between Real Distance and Frame Of Reference ($F_{(1,4,1)} = 15.35$, $p < 0.001$), Group and Frame Of Reference ($F_{(1,4,1)} = 8.35$, $p = 0.01$) and Real Distance, Frame Of Reference and Group ($F_{(1,4,1)} = 3.35$, $p = 0.01$). A post-hoc analysis with Bonferroni correction for multiple comparisons showed a significant difference between distances reproduced from sighted and blind participants only in the external frame of reference task, for all the distances ($p < 0.05$), except for the larger one.

Conclusion

In this study we explicitly investigate the ability of blind and sighted participant to localize sounds within external and body-centered spatial representation, using two different paradigms: auditory space bisection and distance reproduction. We found an impairment only in the early blind group and just for the tasks involving external spatial representations of sounds. This findings, as the one described in in paragraph 2.1.1, can partially help to explain the conflict results about auditory space perception in early/congenital blind people between studies showing at the same time enhanced (Lessard et al., 1998; Röder et al., 1999; Voss et al., 2004) and impaired (Cappagli et al., 2015; Finocchietti et al., 2015; Gori et al., 2014a) spatial auditory performance. The body-centered frame of reference is not compromised by the loss of vision, but the allocentric frame of reference is. Our results support the hypothesis that vision is necessary during development to recalibrate the auditory system so that based on the situation the auditory system became able to shift from a body-centered to an allocentric frame of reference. Lack of vision in early stages of development compromise the calibration impacting on the ability to use external auditory representation, in favor of the use of body-centered reference frame.

Chapter 3

Investigate echolocation with no visual impaired individuals.

Echolocation is the ability to use sound reverberation and spectral coloration to obtain spatial information. Several studies have shown that humans are able to acquire this skill (for a review Kolarik et al., 2014; Supa et al., 1944; Thaler et al., 2011). Echolocation is used by blind individuals, for mainly two reasons: first, to detect objects (even guessing their approximate shape) that is useful for obstacle avoidance needs; second, to estimate essential spatial properties of unknown environments, such as the presence of apertures, the approximate dimensions of an enclosure, and even the material properties of floors and walls that constitute an 'acoustic footprint'. All these information are useful to recognize previously visited locations. Echolocation may be a potential substitute for the vision to calibrate the external space because congenital blinds that use echolocation do not show a deficit in performing an allocentric representation of space (Vercillo et al., 2014). Moreover, it offers a real-life advantage for blind individuals, therefore encouraging social inclusion (Thaler, 2013).

In this chapter, we deepen our knowledge of how echolocation works and test its effectiveness on training procedures with simple spatial tasks. To do that we trained and tested novice sighted individuals. We show that also sighted people can acquire spatial information through echolocation, i.e. localize an aperture or discriminate the depths of an object located in front of them. Then, we identified some kinematic variables that can predict the echolocation performance. Finally, we show that echolocation, not only helps to understand the external space but can also influence internal models of the body-space relation, such as the peripersonal space (PPS). We discuss all these aspects showing that human beings are sensitive to echoes. As a result, we argue that spatial information can be acquired by echolocation when vision is not available also in people that would acquire the same information through vision.

3.1 Echolocation and depth perception

Echolocation is fundamental for navigation mainly because object distance can be inferred to avoid collision. For this reason, some studies have investigated the learning process behind echolocation learning of objects' distances (Schörnich et al., 2012; Wallmeier and Wiegrebe, 2014a), in a virtual echo-acoustic space using pre- recorded noise and echoes produced by a reflective surface. Schenkman and Nilsson (Schenkman and Nilsson, 2010), in their first experiment, investigated how some acoustic information (loudness and pitch) could influence the ability to detect an object at different distances (100, 200 and 300 cm) in a two- alternative forced-choice discrimination task. They found that as long as the pitch component was present, listeners were able to perform the task, even if there was a strong effect of distance to object, i.e. the performance of subjects decreased with increasing distance, highlighting the importance of repetition of pitch for close distances, less than 2m. These finding were confirmed by Rowan et al. (2015). In an identifying right-versus-left lateral position task, using pre- recorded bands of noise, they found that accuracy in judgment decreased with increasing distance, and from distances of 2 or more meters, the participants' performance was random. Moreover, they suggested that performance was due to high- frequency cues and longer auditory signals (400 ms), that improve performance compared to short signals (10 ms), at least for a distance below 1m. If the ability to echolocate is the result of training (and not a combination of visual deprivation and echolocation training), we may also expect to find an improvement of echolocation skills in sighted individuals after training.

In this study, we assessed the ability of novice sighted participants to perform a depth echolocation task and the effect of a brief training in their performance. Conversely to previous studies mentioned above, in this study we decided to test the space into around 1 m and to use real objects, as stimuli, instead of recordings to simulate a situation more similar to everyday life. We divided the sample into two groups: one performed the echolocation task in a reverberant room and the other in an anechoic chamber so that we could test whether the acoustic of the environment can influence the learning process. Moreover, participants could choose between two different ways of producing the echolocation signals: mouth clicks or finger snaps. We found that already at the second session, the participants were able to judge the correct depth of the bar at a rate greater than chance. Improvements in both precision and accuracy were observed in all experimental sessions. More interestingly, we found significantly better performance in the reverberant room than in the anechoic chamber. The type of clicking did not modulate our results. This suggests that the echolocation technique targeting to depth estimation can also be learned by sighted individuals and that room reverberation can influence this learning process.

Participants

For this experiment were recruited a total of 18 sighted participants (9 females and 9 males, with an average age of 29.9, SD = 0.95). We verified that participants exhibited no hearing impairment with a pre-test session. In this session, we used the software EarTest1.0 running on a standard DELL PC. We played tones through a pair of Philips SHL3000PP headphones at right and left ears separately; the tones randomly played, were between 200 Hz and 16 kHz, with an intensity between 10 and 13 dB HL. The intensity levels were preliminarily calibrated by playing the tones through the headphones while recording them with the microphone of a calibrated Delta Ohm sound level meter (HD2010UC/A). The recorded intensity levels were converted from dBA to dBHL according to standard conversion factors. We verified that participants were able to hear the played tones. Participants have no cognitive impairment. All participants gave written informed consent before starting the test. The study was approved by the ethics committee of the local health service (Comitato etico, ASL 3, Genova). The participants received instructions on how to produce the echolocation signals, either by tongue click or a finger snap. They were free to choose the technique they preferred. The echolocation sound was naturally produced, using no external device.

Procedure and apparatus

The task of each participant was to locate the position of a bar of Plexiglas in depth. Participants were divided into two groups. One group performed the task in a reverberant room (4.6m x 6m x 4 m), the other in an anechoic chamber (4.8m x 3.2m x 2.73m). In both rooms, the participants were seated on a chair placed in the middle of the first half of the room. They were facing the center of the room. Participants were instructed on how to generate the echolocation signal using both mouth-click and finger-snaps, and decide which technique used. They practiced for a few minutes to generate sounds as similar as possible to each other.

After the practice session, participants were blindfolded and, to prevented the participants from hearing any acoustic cues about the targets moved by the experimenter, were given ear-bud headphones. Three sessions were performed in two days. The first day participants performed two sessions. The first was a training session. Before each trial, the experimenter randomly placed one of five bars, at one of five possible depths, in front of the participants. Participants were asked to remove the headphones and were given a maximum of the 20s to scan the object in front of them just using the chosen echolocation technique. They had to respond verbally, reporting the depth of the bar with integer numbers from 1 to 5, where 1 was the nearest position and 5 the furthest. In the training session, the participant received a feedback on their response: if the response was correct the experimenter confirmed the position, otherwise, the experimenter gave the correct number associated with the location of the bar. Each depth was repeated randomly 12 times for a total of 60 trials. One session lasted around 90 minutes. After 15 minutes of break, each participant performed the first experimental session. The task and the procedure were the same of the training session, but no feedback was provided. Again, 60 trials were performed for the duration of about 90 minutes. Two days after the first two sessions, the participants were recalled to perform the second and last experimental session, which was identical to the first experimental session in terms of procedure, trial number, and duration.

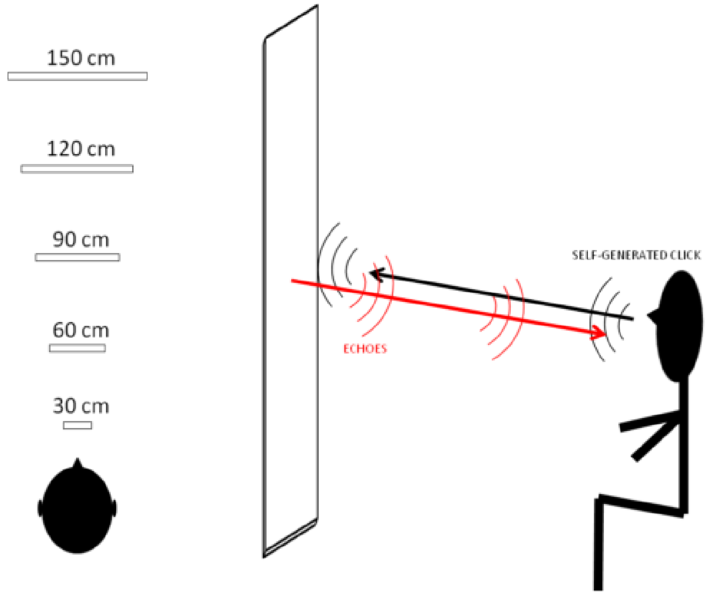


Figure 3-1. Schema of the setup. On the left are illustrated the five difference positions. The first position was at 30 cm (bar size: 40cm x 6 cm) in front of the participant. The second position was at 60 cm (bar size: 72 cm x 11 cm). The third position was at 90 cm (bar size: 108 cm x 16 cm). The fourth position was at 120 cm (bar size: 145 cm x 22 cm). The fifth position was at 150 cm (bar size: 180 cm x 27 cm). On the right, there is the path of the self-generated click (black arrow) reflected by the bar producing way back echoes (red arrow)

The set-up was composed of five rectangular bars of Plexiglas that were presented to all participants with the longer side placed vertically (Figure 3-1). One of the five bars was chosen randomly and located at one of five possible depths from the head of the participants: the first position was at 30 cm (bar size: 40cm x 6 cm) ahead of the participant; the second was at 60 cm (bar size: 72 cm x 11 cm); the third was at 90 cm (bar size: 108 cm x 16 cm); the fourth at 120 cm (bar size: 145 cm x 22 cm) and the fifth position was at 150 cm (bar size: 180 cm x 27 cm). All bars had the same thickness – 0.5 cm. We decided to keep the auditory angle of the bars in the five possible depths constant because a previous study (Milne et al., 2014a) demonstrated that expert echolocators exhibit this same phenomenon in identifying the magnitude of an object through echolocation. We decided to increase the bar size with increasing depth to ensure that the main variable possibly affecting judgments would be distance. When keeping the dimensions of a target reflecting object untouched, while the distance was varied, it was shown that recognition rate drops significantly (Rice and Feinstein, 1965). Rice et al. measured performance of a detection task, i.e. subjects had to report whether a reflecting target was in front of them or not. Moreover, keeping size constant removes a potential confounding factor in depth judgments, as speculated by Teng & Whitney (2011): the subtended angle is a salient metric in size discrimination tasks across distances. Looking the results of Rice et al. (1965), it stands out that the echolocation performance represented by psychometric curves indicated as a function of both distance and target size have something in common: points at equal recognition rate have very similar acoustical angles. However, only target detection skills were considered in the study of Rice et al. (1965) and not distance estimation capabilities. We can, therefore, assume that reflecting objects which respect the same subtended angle is in principle similarly detectable: therefore distance judgments are minimally influenced by target "visibility", rather by all that is left, that is the contribution of echoes. Therefore, the bars used in the experiment subtended a constant acoustical angle of around 10 degrees in azimuth and 62 degrees in elevation. A wooden structure held the bars vertically. Magnets have been applied behind the bars and on the wooden structure to allow a quick change of them during the trails. The floor of the reverberant room was covered by parquet, and turn completely by a 5mm polyester carpet. The walls were concreated, more than 50cm thick and plastered. The room had three doors with solid wood and one window. The ceiling was flat. The T60 of the reverberant room was about 1.4 seconds.

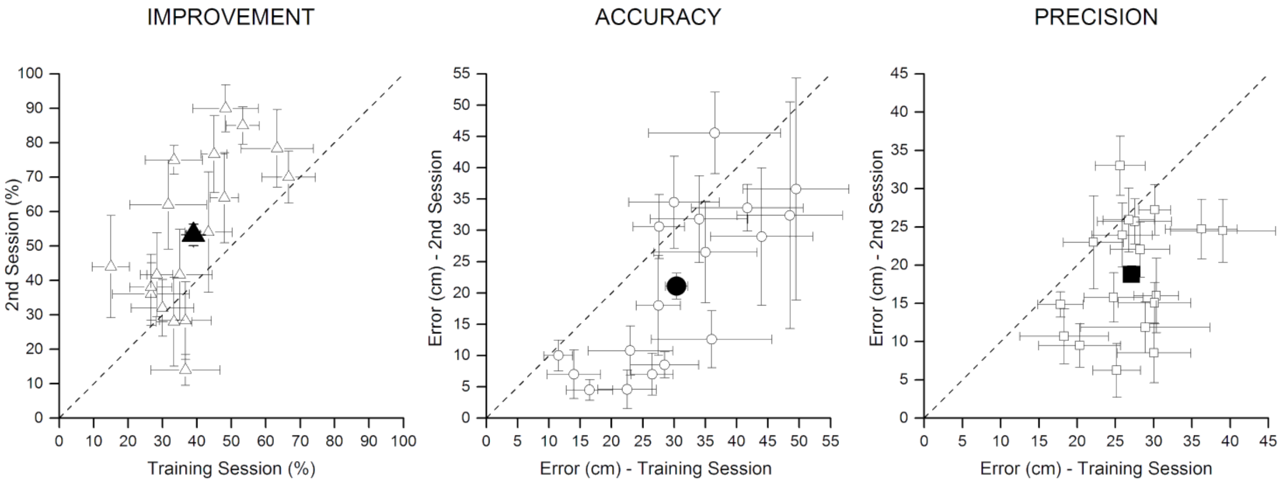


Figure 3-2. On the left are represented the percentage of correct responses obtained in the training session. The other two scatter plots show the accuracy (in the middle) and the precision (on the right)in performing the depth task, independently from the depth. All the graph compared the training session (on the axis) and the second experimental (on the ordinate) sessions. Filled symbols are the average; open symbols are the performance per single participant.

Results

Our data show a progressive improvement in echolocating depth in sighted people after a training session, result consistent with previous studies (Rowan et al., 2013; Schenkman and Nilsson, 2010; Teng, 2011; Thaler et al., 2014b). Figure 3-**2** compares the results of the training session with the second experimental session (filled symbol is the mean; open symbols are the single performances—for the three measurements was conducted a one-way ANOVA with factor Session (training session X first experimental session X second experimental session). We can see that during the session is an improvement not just in the percentage of correct responses (Figure 3-**2** on the left) that is above the chance level of the 20% (F(3,18) = 6.97, p<0.01), but also in accuracy (Figure 3-**2** in the middle) and precision (Figure 3-**2** on the right), which both show a significant improvement (respectively: F(3,18) = 6.29, p<0.01 and F(3,18) = 14.41, p<0.0001). Later, we split the sample into two groups, comparing the performance in the two rooms (Figure 3-3): nine participants performed the task in an anechoic chamber and nine in a reverberant room. We calculated the average ratio of improvement by dividing the percentage of correct responses of each experimental session by the percentage of correct responses to the training (Figure 3-3). We run a mixed model two-way (3 x 2) ANOVA with within factor Session - training Vs 1st Session Vs 2nd Session - and between factor Type of room - anechoic Vs reverberant room), for the anechoic chamber (in blue) and the reverberant room (in red). We found one main effect between the sessions (F(4,18) = 17.03, p<0.001), but not between the type of rooms (F(4,18) = 0.001, p = 0.98). Concerning accuracy (Figure 3-3 B**)** and precision (Figure 3-3 C) of the error of judgment obtained

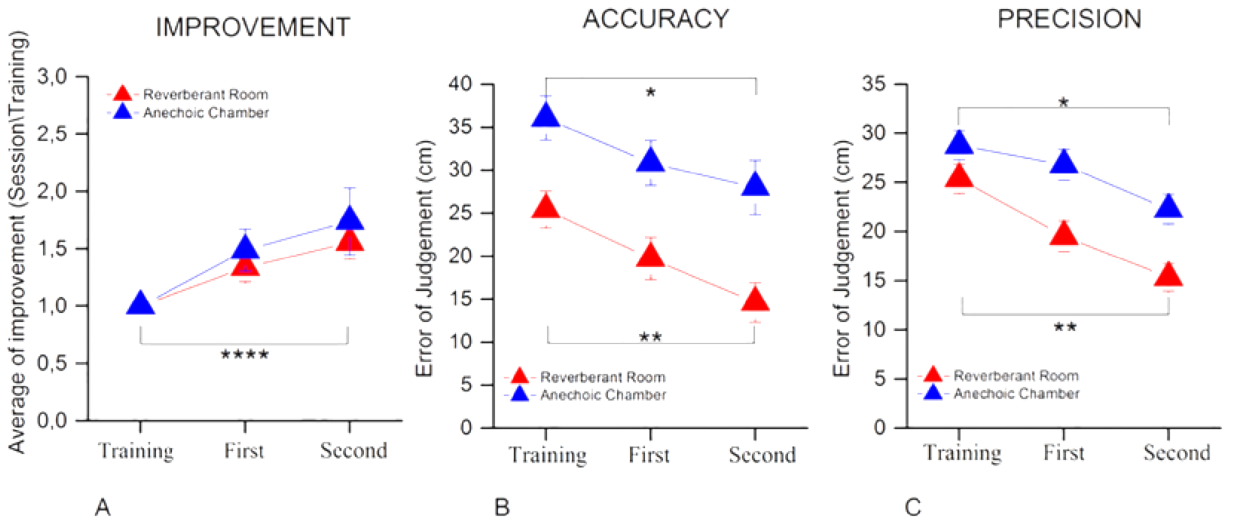


Figure 3-3. In these plot are compered the results of the group in the reverberant room and the group in the anechoic chamber. (A) Shows the average ratio of improvement of the performance in both the experimental sessions. It compares the improvement for the type of room in which the participants performed the task: anechoic chamber (blue symbols) and reverberant room (red symbols). The improvement was obtained by dividing the results of all the sessions by the result of the training session. (B) The scatter plot shows the accuracy with which the task was carried out in all the sessions in the anechoic chamber (blue symbols) and in the reverberant room (red symbols). (C) The plot show the average error of judgment in precision for each rooms: anechoic chamber (in blue) and reverberant room (in red). (****)Indicates a significant difference, $p < 0.0001$. (**) Indicates a significant difference, $p < 0.01$. (*) Indicates a significant difference, $p < 0.05$.

by the participants in the anechoic chamber and the reverberant room, a mixed model three-way (3 X 2 X 5) ANOVA was run (for both precision and accuracy) with within factor Session -training Vs 1st Session Vs 2nd Session—and between factor Type of room - anechoic Vs reverberant room - and Position - 1st position Vs 2nd Position Vs 3rd Position Vs 4th Position Vs 5th Position). We found a significant difference for both values between sessions (accuracy, $F(6,54) = 15.0215$, $p<0.0001$; precision, $F(6,54) = 14.42$, $p<0.0001$), but in this case there was also a significant difference for the type of room in which the task was per- formed (accuracy, $F(6,54) = 6.0552$, $p<0.05$; precision, $F(6,54) = 5.87$, $p<0.05$), which shows that the reverberant room, is the best environment for learning echolocation. As well as analyzing the performance obtained in the two rooms, we investigated the results for the different types of techniques used to produce the echolocation signal. The sample was divided into two groups of nine participants each: those that decided to echolocate using mouth-click and those that used finger-snap. We calculated the average ratio of improvement by dividing the percentage of correct responses of each session by the correct responses in the training (Figure 3-4 - a mixed model two-way (3 x 2) ANOVA with within factor Session - training Vs 1st Session Vs 2nd Session - and between factor Type of room - anechoic Vs reverberant room) for the mouth-click (in green) and the finger-snap (in violet). As shown by the previous data, also, in this case, a significant effect between the sessions was found ($F = 17.03$,

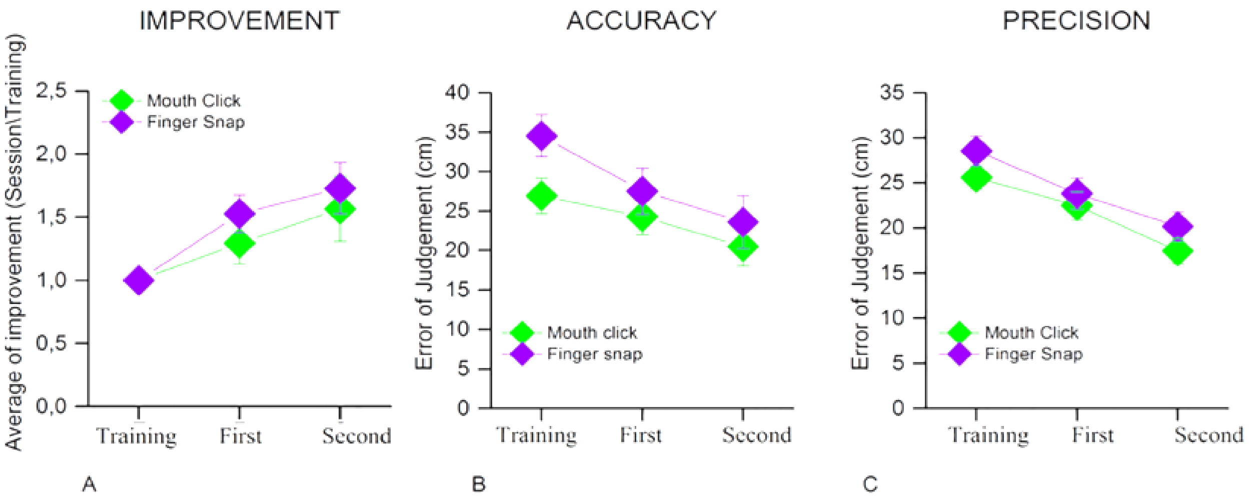


Figure 3-4. In these plots are presented the results compered the group using mouth clicks and finger snaps. (A) Shows the average of improvement of the performance in both the experimental sessions. It compares the improvement for the type of click used by the participants in the task: mouth-click (green symbols) and finger-snap (violet symbols). The improvement was obtained by dividing the results of all the sessions by the result of the training session. (B) The scatter plot shows the accuracy with which the task was carried out in all the sessions using mouth-clicks (green symbols) and finger-snaps (violet symbols). (C) The bars are the average error for precision for each the five positions of the task using mouth-clicks (green symbols) and finger-snaps (violet symbols).

$p<0.001$), where the performance in the second experimental session we significantly better compared to the training session. The type of click, however, was not shown to affect the results ($F = 1.78$, $p = 0.19$). Conversely, accuracy (**Figure** 3-1 B) and precision (Figure 3-4 C) of the error of judgments obtained by the participants that used the finger-snap or the mouth-click to echolocate did not indicate a significant difference between the two types of technique used (respectively $F(6,54) = 1.06$, $p = 0.318$ and $F(6,54) = 0.71$, $p = 0.411$). However, a significant effect between sessions (accuracy, $F(6,54) = 15.19$, $p<0.001$; precision, $F(6,54) = 13.72$, $p<0.001$) was present (a mixed model three-way (3 X 2 X 5) ANOVA was run with within factor Session - training Vs 1st Session Vs 2nd Session - and between factor Type of room - anechoic Vs reverberant room - and Position - 1st position Vs 2nd Position Vs 3rd

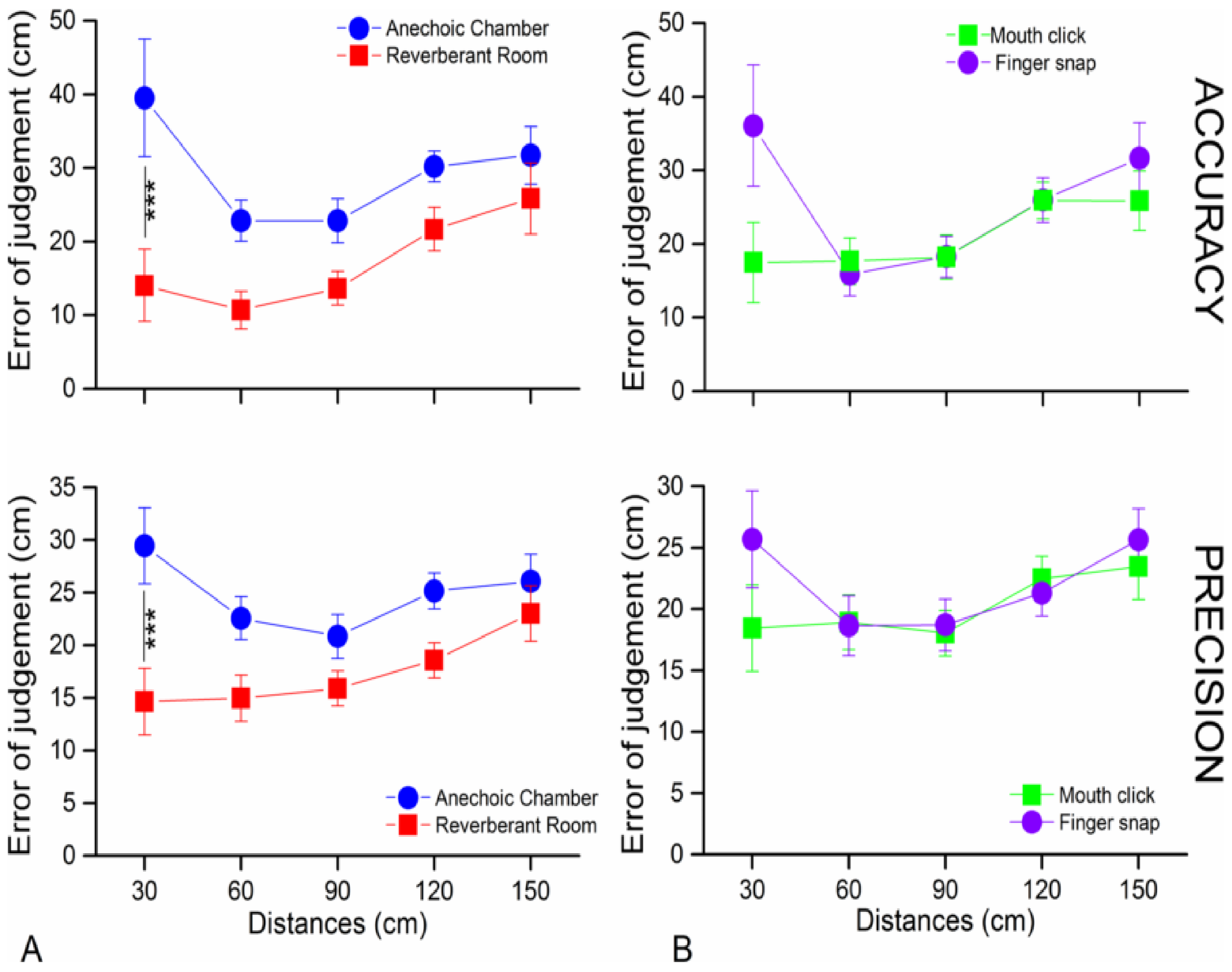


Figure 3-5. Accuracy and precision for each depth for the two experimental sessions. (A) Shows the average error for accuracy (above) and precision (below) in the anechoic chamber (in blue) and reverberant room (in red). Comparing each depth in the two rooms the only significant difference is for the depth at 30 cm. (B) The scatter plots represent the average error for accuracy (above) and precision (below) for each position divided for the type of click. (***) Indicates a significant difference ($p < 0.001$).

Position Vs 4th Position Vs 5th Position). In Figure 3-5, we investigated whether there were differences between the five depths used for the two pair of groups compared (anechoic vs. reverberant room and finger snap vs. mouth click) in precision and accuracy, taking into account just the two experimental sessions. For the first group (anechoic vs. reverberant room - Figure 3-5 A) we found a significant difference between the anechoic chamber and the reverberant room for both accuracy (F(5,18) = 10.59, p = 0.003) and precision (F(5,18) = 10.07, p<0.004) and also between the different depths (accuracy F(5,18) = 5.3, p<0.01; and precision F(5,18) = 3.8, p<0.01). In particular, the data show that participants found it easier to detect the nearest position (30 cm) in the reverberant room than in the anechoic chamber (p<0.001). For the second pair (finger snap vs. mouth click - Figure 3-5 B), the type of click used did not significantly affect the results (accuracy F(5,18) = 1.15, p = 0.29; and precision F(5,18) = 0.43, p = 0.51), but there still remained a significant effect for depth (accuracy, F(5,18) = 5.38, p<0.001; and precision, F(5,18) = 3.66, p<0.01). In addition, a significant interaction between type of click and position was found for accuracy (F(5,18) = 3.19, p<0.05), but not for precision (F(5,18) = 1.53, p = 0.2).

Conclusion

In this experiment we investigated three aspects: 1) whether sighted people can be trained to perform a depth echolocation task; 2) whether there is an influence of the environment in which the task is performed (namely comparing results obtained in an anechoic chamber and in a reverberant room); 3) whether there is a difference between using mouth clicks or finger snaps to produce the echolocation signal.

Results showed that sighted people are able to perform a depth echolocation task after just around one hour of training in line with previous studies that investigated learning skills in sighted individuals (Rosenblum et al., 2010; Schenkman and Nilsson, 2010; Teng, 2011; Thaler et al., 2014b). Thanks to the training there is a general improvement in the performance, participant more precise and accurate.

About the difference between anechoic and reverberant room, we found that there is no difference in the percentage of correct responses, but, the interesting point is that in the reverberant room participants are more accurate and precise compared to the group that performed the task in the anechoic chamber. A possible explanation is that the reverberant room provides more cues comparing the anechoic chamber, i.e. the reverberation per se. While in the anechoic chamber there is just one set of information to localize the silent object, i.e. the direct path of the echoes (early reflections) that is the reflection of the sound on the object, in the reverberant room there is also a second set of echoes, the ones produced by the sound reflecting on the walls (late reflections). All the echoes together change based on the location of the object, suggesting that some acoustical characteristics, such as late echoes and spectral coloration of the reverberant room, can be as important as the early echoes, which are known to be interpreted by our brain in terms of binaural cues (Libbey and Rogers, 2004; Shinn-Cunningham et al., 2005). The binaural cues, however, in our setup, are arguably not mainly responsible for the difference between the two rooms, because the reflecting objects are located in front of the participant. When objects are facing the participant, the time lag between the right and left ear (Interaural Time Difference) of the main reflected sound is almost zero. As well, the difference in sound intensity impacting the ears (Interaural Level Difference) is almost zero. Finally, the energy of the direct path does not approximately depend on distance, since we imposed acoustic size constancy, therefore it may not have modulated our results. That is, the information from the direct path in both environments in this study is small. Therefore, information must have come from all that was left: the difference we observe the two environments can be ascribed to late echoes, to the mixed binaural cues that they elicit when sound bounce in every direction (therefore not in front of the participant) and to the possibly different spectral coloration cues that these echoes, together, cause when putting the objects at various distances.

Finally, we found that there is not a significant difference between the two techniques used to produce the clicks – mouth click and finger snaps. From these results we can infer that probably the manner in which the sound is produced by novice echolocators does not matter in a depth task, but rather the amount of available environmental cues is the key factor (i.e. room reverberation).

3.2 Kinematics of echolocation movements

Echolocation is the ability to acquire spatial information from the reflection and the timber of sounds. It is well known that humans can develop such skill (Kolarik et al., 2014; Supa et al., 1944; Thaler and Goodale, 2016), which can be learned by blind (Milne et al., 2014b; Thaler et al., 2014a) and sighted individuals (Teng, 2011; Tonelli et al., 2016). In the last few years a number of studies are investigating the underpinning of sounds that can be used for locomotion in absence of vision and most of these studies have in common the use of echolocation. Rosenblum et al. (2010) showed how sighted blindfolded participants were able to detect and walk up to an estimated position of a wall, finding that participants were more accurate when emitting sounds during motion than when standing still, for some distances.

Kolarik et al. (2016), assessed the ability of blindfolded sighted people to detect and circumvent an obstacle just using mouth click sounds, compared to visual guidance. They showed that auditory information was sufficient to guide participants around the obstacle without collision, but there was an increase of movement time and the number of velocity corrections compared to visual guidance. Moreover, in a second study, Kolarik et al.(2017), used the same task to compare the performance between blindfolded sighted, blind non-echolocators and one blind echolocator using both self-generated sounds and an electronic sensory substitution device (SSD). They found that using audition, blind non-echolocators navigated better than blindfolded sighted with fewer collisions, lower movements times, fewer velocity corrections and grater obstacle detection range. Instead, the performance using a SSD between the two groups was comparable. The expert echolocator had better performance than the other two groups using self-generated clicks, but was comparable to the other groups using SSD. All three groups gave 100% correct responses. All these findings support the hypothesis of *enhancement*: vision loss leads to enhanced auditory spatial ability due to an extensive experience and reliance on auditory information (Kolarik et al., 2013; Voss et al., 2015) and cortical reorganization (Collignon et al., 2013; Kupers and Ptito, 2014; Voss and Zatorre, 2012). Similar results were found by Fiehler et al. (2015): when listening to pre-recorded binaural echolocation clicks generated while a person was walking along a corridor, blind expert echolocators performed better than sighted novice participants in judging the main direction of the corridor (left, right or straight ahead). Even if sighed participants received a training, their performance was around chance level.

Another important point is that the head movements during echolocation seems to have a crucial role (Milne et al., 2014b). Wallmeier and Wiegrebe (2014a), showed how head rotations during echolocation can improve performance in a complex environmental setting. They also reported that during echolocation participants tend to orient the body and head towards a specific location (Wallmeier and Wiegrebe, 2014b).

Here, we used the task of Fiehler et al. (Fiehler et al., 2015), but instead of using pre-recorded echolocation clicks, we asked participants to freely perform the task in a real environment, all by recording their body motion. Specifically, we installed inside a reverberant room a real corridor made of sound-reflecting panels. We asked participants to judge one spatial property of the corridor, i.e. whether it was turning left, right or had a dead end. Importantly, participants were free to stop anywhere they wished when guessing the shape of the corridor.

First, we wanted to test whether novice blindfolded sighted participants were able to perform such a task. We also wished to compare whether the performance obtained in the study of Fiehler et al. (2015) was possibly influenced by the use of binaural recordings. We hypothesized, in particular, that understanding spatial properties of unknown spaces is modulated by behavioural variables, such as body motion. If this is true, then observing echolocation in real setups can extend the knowledge - about how this skill is developed - with information that virtual setups a priori may exclude. More generally, we sought for body movements that can be overt signs of optimal echolocation skills.

To assess that, we used a motion capture system to record and code the kinematics of the participants who walked along a corridor while echolocating. First, we took into account several behavioural variables: the average and variability of velocity, the duration of motion, the position of each participant in the room at the moment of the response, and the motion of the head; then we tested whether these variables correlated with the percentage of correct responses. Finally, we derived a predictive model that shows how the probability of correct guess is accounted for by the variables explaining most of the behavioural variance.

Participants

Nine sighted participants (4 females, with an average age of 27.5, SD = 7) were recruited to participate in the experiment. All participants gave written informed consent before starting the test. All participants were submitted to an audiometric test to check for possible hearing impairments. The test was performed automatically by an audiometer (Amplaid A1171), by presenting tones of increasing intensity between 200 Hz and 12 KHz at 20 dB, while asking the participant to press a button when the tone became audible. One of the participants did not pass the test and was excluded from the experiment. None of the participants had prior experience in using self-generated sounds to perceive objects. The study followed the tenets of the Declaration of Helsinki and was approved by the ethics committee of the local health service (Comitato Etico, ASL 3, Genova).

Procedure and apparatus

The task was to judge one spatial property of the corridor, i.e. whether it was turning left, right or had a dead end.

First, participants were instructed on how to generate echolocation signals using mouth clicks. They practiced for few minutes to generate sounds as similar as possible to each other. Before entering the room of the experiment, all participants were blindfolded, to prevent them to gain prior knowledge of the structure of the room and the setup.

First, each participant performed a training session, in which they were brought by the experimenter to the starting point (see Figure 3-**6** B) of the corridor and they had to walk along the corridor, trying to walk straight, just using mouth clicks. They had to reach a stopping point (see Figure 3-**6** B), located at around 1 meter from the wall. From that position they were instructed to walk through the corridor, having 20 s to understand how the corridor was ending: opened to the left, to the right or closed from both sides. The participant was free to move: however, in this training session, a heavy box (0.8x0.5mx0.5m) was placed on the ground at the ‘End’ point (see Figure 3-**6** B), 1m from the end wall in concrete, to force the participant to stop and express a guess on the shape of the corridor.

The trial was considered null and excluded from the analysis when the participant did not respond within 20 seconds. Instead, if the participant touched the walls of the corridor, the trial was repeated. Each participant performed 27 trials.

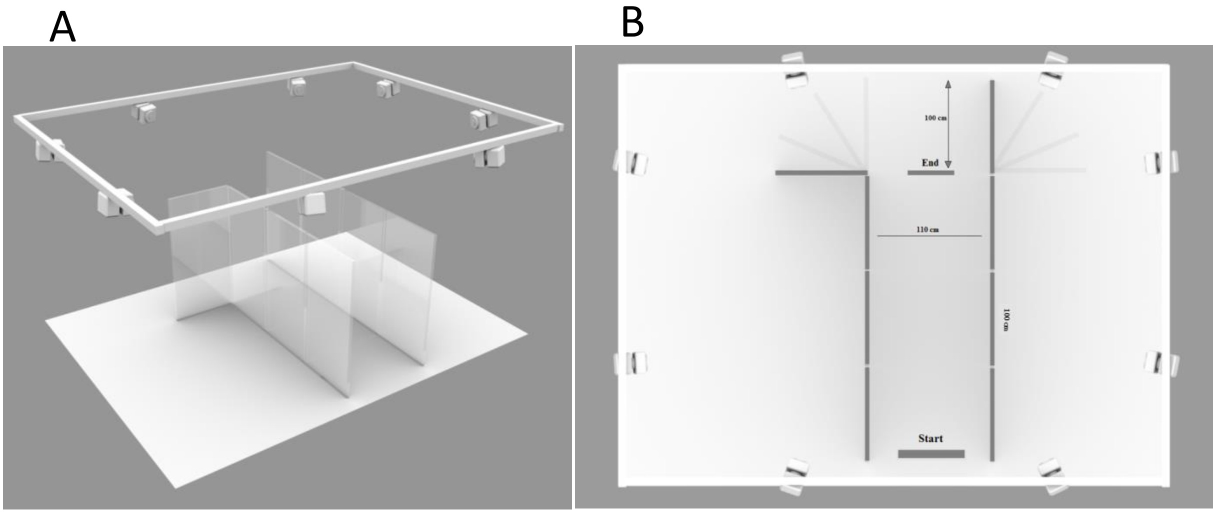


Figure 3-6. Experimental set-up. (A) Show the position of the corridor inside the room and the position of the Vicon cameras. (B) View from above of the corridor.

The experimental and the training sessions were identical, except for the stop point. The stop point was not present in the experimental session: the experimenter asked each participant to stop as soon as they understood the shape of the corridor and to give right away the answer. The trial was considered incorrect whether the participant touched the walls of the corridor, or reached the end of the corridor without giving any response or took too much time to give an answer after they stopped. This happened in 12% of our trials. Also in this session, each participant performed 27 trials.

The task was performed in a reverberant room (4.6mx 6mx 4 m). The floor of the room was covered with parquet and completely covered by a 5mm polyester carpet. The walls were concrete, more than 50cm thick and plastered. The room had three exits: three doors in solid wood, and one window, covered by solid wood panels. The high ceiling (about 4 m) was flat. The T60 of the reverberant room was about 1.4 seconds. The corridor was composed of 8 panels of poly-methyl methacrylate (PMMA). They were 2m high and 1m wide and were placed vertically next to each other. Each panel had been supported by a metal frame positioned outside the corridor, so as not to interfere with the task or with sound reflections. The metal frame was provided with wheels to facilitate the movement of the panels between the trials.

The corridor was created along the smaller side of the room, so to use one of the walls of the room at the bottom of the corridor; instead to create the side walls we used the panels of PMMA, 4 for each side (see Figure 3-**6**A). The corridor was 4m long and 1.1m wide and was set in three different shapes: opened to the left, to the right or closed from both side (see Figure 3-**6**B for exact dimensions).

To record the kinematics of the body we used an infrared camera motion system with eight cameras (frame rate 100 Hz, Vicon Motion Systems, Oxford, UK). The cameras were placed along the perimeter of the room at about 3 meters high (see Figure 3-**6**), so that at least 3 cameras could focus on every corner of the corridor at the same time to ensure optimal recordings. Each participant was

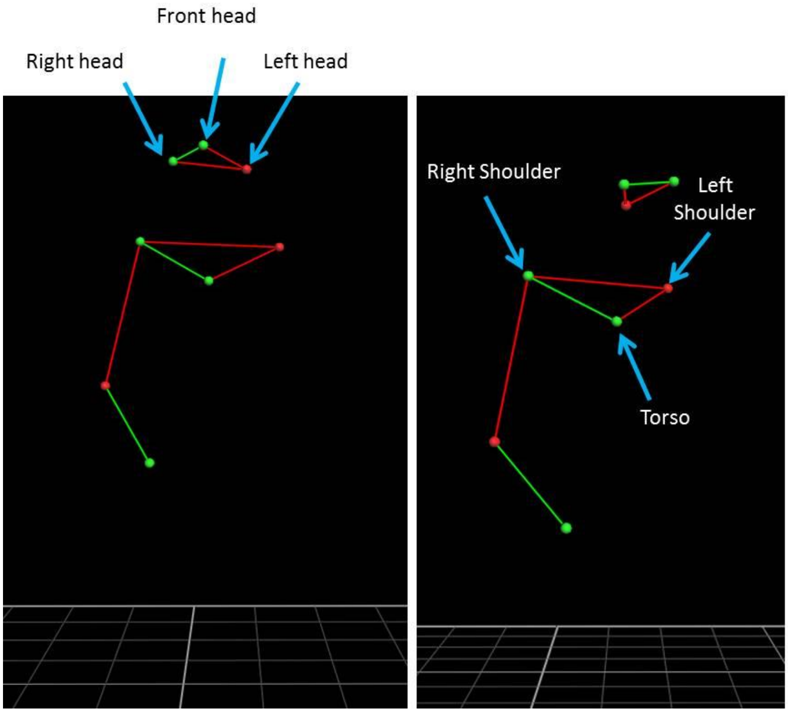


Figure 3-7. Example of the position of the marker on the body. Vicon representation.

outfitted with eight lightweight retro-reflective hemispheric markers (1 cm in diameter). We arranged three markers on the head to form a triangle with the marker on the forehead as a tip; one marker on each shoulder, one at the level of the breastbone, one on the right elbow and one on the right wrist (see Figure 3-7). A model of each subject's marker placement than was calibrated using Vicon's Nexus® software. However, the markers on the elbow and the wrist were not used during the data analysis.

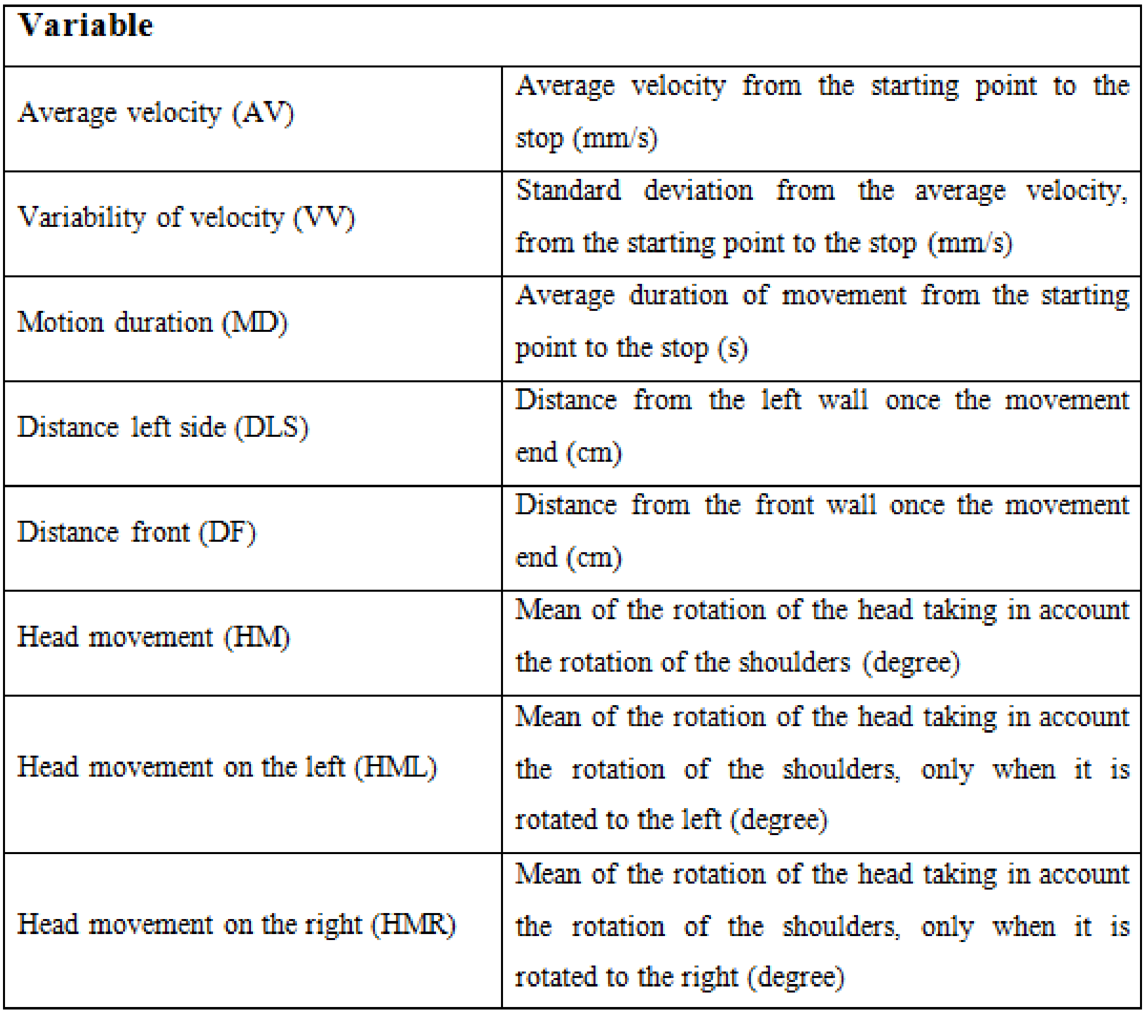
After the data acquisition, each trial was individually inspected to check the correct uploading of the model after the pre-processing. We applied a low-pass Butterworth filter with a 6 Hz cut-off.

Variables related to head and body movements were computed with custom-written Matlab® scripts. Definitions of the variables are presented in Table 3-1.

Specifically, AV and VV were computed by excluding the trajectory of the participants: only the starting point and the end point location were considered and divided by MD.

Then, DLS and DF helped to reconstruct where the participant stopped with respect to the end of the corridor, specifically highlighting if the stop point was closer to either wall.

Finally, HM, HML and HMR accounted for head motion, however differently: HR helped to give a general idea of the amount of head movement made by the participant, whereas HML and HMR informed about which portion of space is explored.



Variable	
Average velocity (AV)	Average velocity from the starting point to the stop (mm/s)
Variability of velocity (VV)	Standard deviation from the average velocity, from the starting point to the stop (mm/s)
Motion duration (MD)	Average duration of movement from the starting point to the stop (s)
Distance left side (DLS)	Distance from the left wall once the movement end (cm)
Distance front (DF)	Distance from the front wall once the movement end (cm)
Head movement (HM)	Mean of the rotation of the head taking in account the rotation of the shoulders (degree)
Head movement on the left (HML)	Mean of the rotation of the head taking in account the rotation of the shoulders, only when it is rotated to the left (degree)
Head movement on the right (HMR)	Mean of the rotation of the head taking in account the rotation of the shoulders, only when it is rotated to the right (degree)

Table 3-1. Assessed dependent variables and their descriptions.

Results

We analyzed the kinematics of head and body movements for the experimental condition only. To understand the relation between the behavioral variables, we run a factorial analysis to test the correlation (see table 1). For the factorial analysis, we used a *varimax rotation* (Kaiser, 1958) based on the sum of the variance of normalized body weight squares. We extracted four factors that explained most of the variance in the data (64.2%, $\chi^2 = 2.7$, $p = 0.26$). Figure 3-**8** shows the outcome of the factorial analysis, namely the weights of the changes of all the variables on the four factors, i.e. the relationship of each variable to the underlying factor. The first factor included mainly the variables AV, VV, and MD, that are variables related to the time dimension (TIME factor). The second factor is mainly influenced by variables related to the exploration with the head (HEAD EXPLORATION factor): HML, HMR, with a contribution from the spatial factor DF. The third factor is almost purely related to head movements (HEAD factor). Instead, the fourth factor is related to the space domain (SPACE factor) because of the strong weight of the DF variable.

Considering performance, we checked whether the percentage of correct responses was no chance level for both the training and the experimental session (Figure 3- 9). The percentage of correct responses in the training session was 68.28% (t-test, $t_7 = 6.7$, $p < 0{,}001$) and for the experimental session was 58 % (t-test, $t_7 = 2.71$, $p = 0{,}03$), both significantly above the chance level. Moreover,

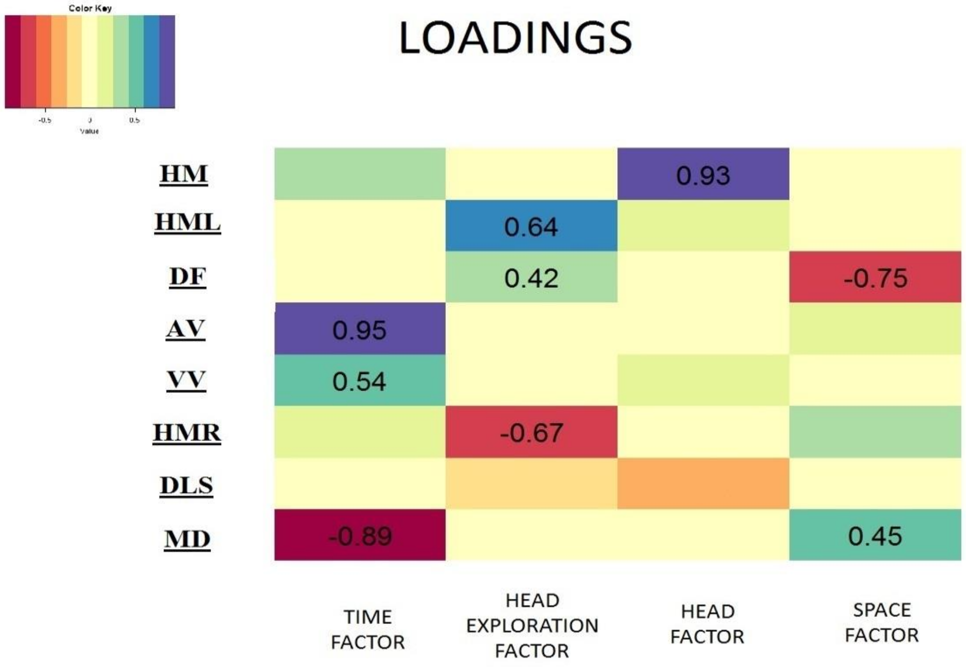


Figure 3-8. Outcome of the factorial analysis. Weights of each variable on each factor. Are consider just weights over 0.4

we calculated whether there was a correlation between the performance and the type of shape of the corridor. One-way ANOVA with factor SHAPE did not show any significant difference ($F_{2,14} = 1.48$, $p = 0.26$).

Then we tested whether the kinematics variables were related to the participants' ability to echolocate. To this aim, we used the scores of each factor obtained from the factorial analysis and the variable CORRIDOR'S SHAPE (open to the left, open to the right, closed) as independent variables in a logistic regression model (Hosmer and Lemeshow, 2004) with RESPONSE (correct and incorrect) in the echolocation task as dependent variable.

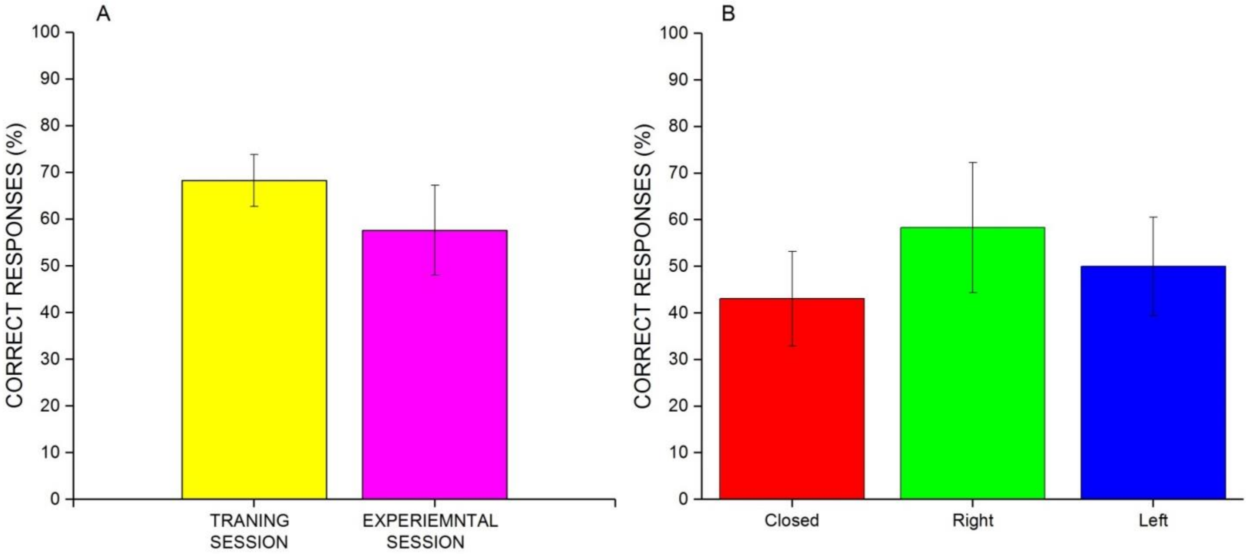


Figure 3- 9. Percentage of correct responses for the echolocation task. The main bar plot represent the results for the training session (yellow) and the experimental session (in magenta). In the small bar plot are represented the percentage of correct responses in the experimental session for each shape of the corridor closed (in red), right (in green) and left (in blue).

We found a significant main effect for factor HEAD EXPLORATION ($\chi^2 = 8.027$, $p = 0.004$), factor HEAD ($\chi^2 = 4.54$, $p = 0.03$) and factor SPACE ($\chi^2 = 14.14$, $p = 0.0001$). Only one significant interaction was found CORRIDOR'S SHAPE x factor HEAD EXPLORATION x factor HEAD x factor SPACE ($\chi^2 = 6.15$, $p = 0.04$). Given the graphics limitation in representing the significant interaction, in Figure 3- 10 we plotted the probability of correct response predicted by the model for each level of the variable CORRIDOR'S SHAPE in the relation of every single factor, i.e. the variation of the slope is related to the variation of the probability to give a correct response.

Importantly, the strongest predictor of performance was the SPACE FACTOR. Specifically, the participants stopped at 0.65 m (sd = 0.29) from the end of the corridor.

More specifically, from figure 5 we derive that the highest guess rate probability is associated with negative values of the SPACE FACTOR, therefore with larger values of the DF variable and lower values of the MD variable: the earlier the spontaneous stop point, the better the guess. We calculated whether there was a significant difference of DF depending from the shape of the corridor (Figure 3-**11**). One-way ANOVA with factor SHAPE did not show any significant difference ($F_{2,14} = 2.35$, $p = 0.12$).

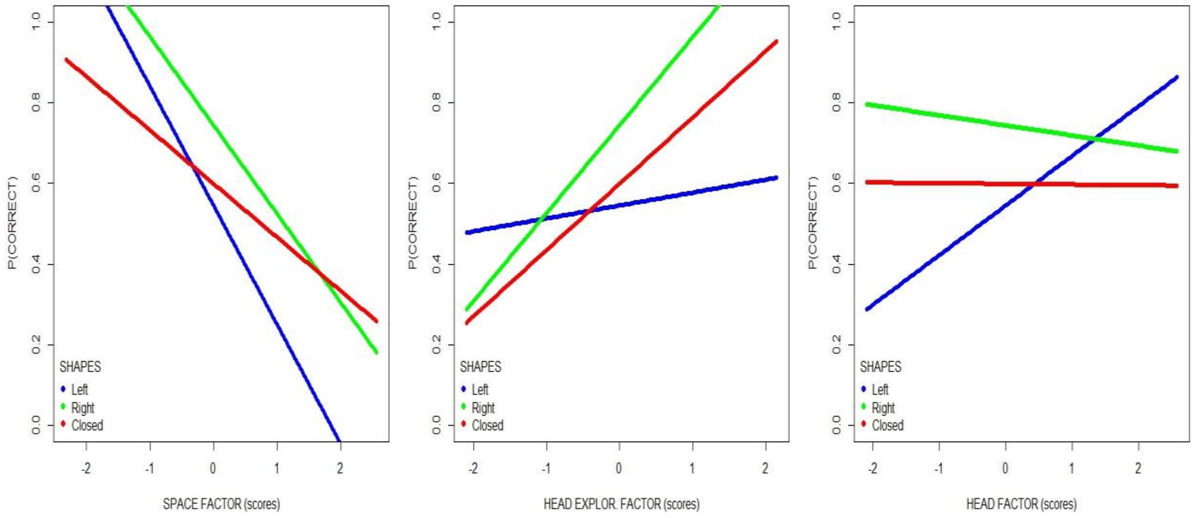


Figure 3- 10. In these graphs are plotted the probability of correct response predicted by the model for each level of the variable CORRIDOR'S SHAPE in relation of the factor present in the significant interaction of the logistic regression.

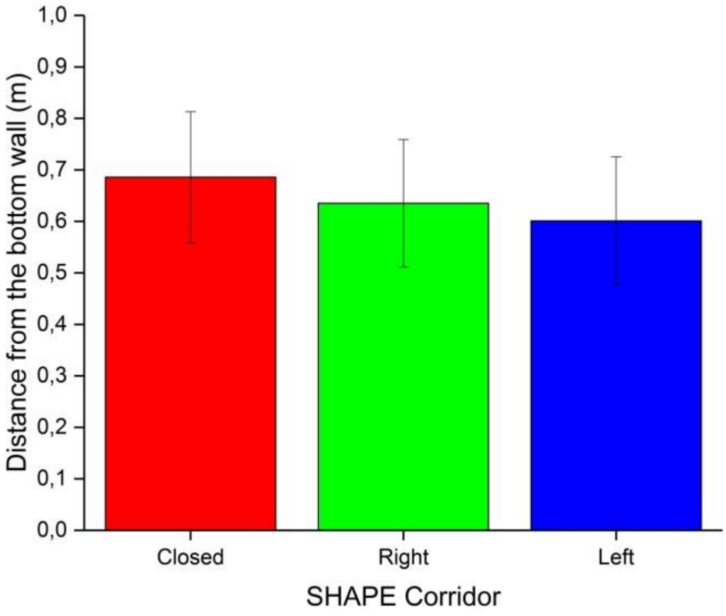


Figure 3-11. Average distance from the bottom of the corridor for each corridor Shapes

Conclusion

The novelty of this study is the identification of some behavioral underpinnings of echolocation: we found a direct correlation between the ability to perform an echolocation task and how the body of naïve echolocators moves in space.

The major point of this study was to test: 1) whether also sighted people are able to perform an echolocation task in a complex environment, as much ecological as possible; 2) whether some behavioral variables (table 1) regarding how naïve echolocators move into such environment might be correlated with a performance variable.

Previous studies already have shown that sighted people were able to learn echolocation in a brief amount of time, by performing tasks as detection, size perception or acuity discrimination (Schenkman and Nilsson, 2010; Teng, 2011; Thaler et al., 2014b; Tonelli et al., 2016) that involve sound reflections from a restrained set of objects. None of these studies tested the ability to perform in more complex scenarios, with reflecting walls in multiple configurations and freedom to move the whole body.

The first result is that also sighted people are able to perform a complex auditory task such as understanding the shape of a corridor. Unlike the behavioral results of Fiehler et al. (2015), where the performance of sighted people was at chance level, we found that sighted are able to accomplish such a task.

Probably the different result is due to the modality in which the task was completed: in Fiehler's study, binaural recordings were used (since the main purpose of the study was to investigate the neural correlate using fMRI); instead, in our study the participants could link acoustic, proprioceptive and vestibular perceptual cues, therefore possibly integrating multiple sources of information (Wallmeier and Wiegrebe, 2014a) and sensory-motor association (Flanagin et al., 2017).

Based on our results we identify three main factors the might influence the echolocation performance: time, space and head motion.

Time is not important

Our first behavioral factor was related to time. It positively correlated with the average velocity and its variations and, as expected, negatively with the duration of motion.

We did not find an influence of completion time in the number of correct responses, that is fast body motion seems not related to a better understanding of an unknown environment. A similar result appears when evaluating travel aids such as white canes, that on one hand reduce collisions but do not necessarily decrease task completion time (Kim and Cho, 2013). As well, completion time seems the weakest predictor of performance when both blind and visually impaired persons get explicit feedback on spatial properties of unknown paths (Kalia et al., 2010). Considering that head motion seems important to correctly guess the corridor shape, we interpret that exploring the acoustical properties by turning the head takes time: the amount of information with head exploration may force to pay a price in terms of completion time, that therefore seems not relevant as performance predictor. Further investigation on how effectively the body moves, or stops and then spends time while acquiring information, is necessary to clarify this aspect. On the same line, velocity seems not related to performance: our two variables related to the average body velocity and its variations are only accounted for by the time factor, which does not predict performance. As a counter-proof, they are absent from any other factor having an effect on performance.

Head motion appears crucial

Our second behavioral factor was related to head exploration: it is positively correlated with the average angle when the head is rotated to the left of the body midline (i.e. net of how the shoulders are rotated) and, as expected, negatively when the head is only rotated to the right; interestingly, the factor accounts for almost equivalent amounts of these two variables, meaning that the influence of head motion seems not to be biased by some sort of lateralization. This well reflects our experimental setup, where participants started from the center of the corridor and had an equal chance of finding a right-ended or left-ended corridor. Intuitively, they did not need to turn their head more to the right or to the left. When investigating the link between head motion and performance, higher values of such factor reflect a probabilistic higher understanding of the environment; conversely, when values of the factor become negative, the guess rate is close to chance level: the wider the lateral head movements, the better the guess.

Similar considerations hold for the third behavioral variable, mainly related to the mean head rotation angle, that is the only variable with a significant weight. This factor highlights the importance that head movements have during echolocation in line with previous results independently from the environment and the kind of task performed (Milne et al., 2014b; Wallmeier and Wiegrebe, 2014b). Taken together, these results are important because they emphasize that the head has a key role. Active head exploration seems therefore necessary to understand structural properties of echolocation.

Space: we don’t stop by chance

Interestingly, we found a significant link between the spontaneous stop point and the probability of correct guessing, with people stopping earlier as more reliable predictors of the corridor shape.

Therefore, an external observer (for example a rehabilitation practitioner) may infer whether a blindfolded person has well understood the environment by only looking at where decisions are taken, no matter the response. This result may serve as a guideline for orientation and mobility practitioners and in general to gain knowledge about the link between the behavior of persons in the dark and their understanding of where they are.

The average distance from the bottom of the corridor was 0.65 m (sd = 0.29): Interestingly, almost the same distance was found by Kolarik at al. (2016) when the obstacle was located in the midline (0.61 m).

Our task was different than in Kolarik at al. (2016): in that task the person had to stop when detecting an obstacle (assumed to exist), while in our task one or more lateral obstacles (i.e. the presence or absence of one or two apertures on the end sides of the corridor) could be present or not, while the end of the corridor was always in a fixed position. Nevertheless, we can start assuming that the distance to which spatial properties of an object reveal themselves by echolocation may not be a function of the sound environment. Further research is necessary to discover acoustical spatial invariants, possibly linked to gestures (Fowler et al 1994).

Finally, the kind of configuration of the corridor did not have a main effect on performance. The shape of the corridor, therefore, did not significantly bias the guess rate. However, we found an interaction with all the factor influencing it: the structure of the environment seems to have an influence on how the body moves, but not on the final outcome of the task. This is interesting since it could hint that body motion reflects spatial structures *before* these are explicitly externalized.

Purely looking at performance, then, in both our training and experimental session the percentage of correct guesses was on an average double that chance. Although not significant, the experimental session exhibited a slightly lower performance due to the absence of the physical stop constraint. Therefore, free motion seems to add ecological validity to our setup without paying a price in terms of understanding of spatial properties.

3.3 Echolocation and multisensory interaction

Space is a construction of our brain and mind. Several lines of evidence show that our brain continuously generates multiple neural representations of coexisting spaces, depending on incoming sensory inputs, action/intention, and reference frames (Holmes and Spence, 2004; McNaughton and Nadel, 1990; Pasqualotto et al., 2013b). An interesting spatial representation, which is nowadays attracting a renewed interest, is the peripersonal space (PPS), i.e. the space immediately surrounding the body (Cléry et al., 2015; Dijkerman and Farnè, 2015; Ladavas and Serino, 2008; Rizzolatti et al., 1997; Serino, 2016). Studies show that PPS is represented via the integration of somatosensory stimuli from the body with visual (Làdavas et al., 1998; Macaluso and Maravita, 2010) or auditory stimuli (Occelli et al., 2011) from the environment, when they are presented at a limited distance from the body, which defines the extent of the PPS. Interestingly, PPS representation has a direct link to the motor system, as stimuli presented within the PPS prime defensive (Graziano and Cooke, 2006) or approaching (Rizzolatti et al., 1997) body actions (Avenanti et al., 2012; Cardinali et al., 2009; Makin et al., 2009; Serino et al., 2009).

An important property of PPS representation is that it dynamically modifies through experience, i.e., by short (Canzoneri et al., 2013; Farnè and Làdavas, 2000; Holmes et al., 2004; Holmes and Spence, 2004) and long term (Serino et al., 2007) tool use, social interaction (Ferri et al., 2013; Heed et al., 2010; Pellencin et al., 2017; Teneggi et al., 2013) and potential movements (Brozzoli et al., 2010; Noel et al., 2015).

In this study, we investigated whether a novel form of exploring and interacting with the environment, via auditory information, shapes PPS representation. To this aim, we used echolocation, a technique used by some blind individuals to substitute vision in perceiving aspects of the surrounding environment.

To test whether an echolocation training can modify PPS, we evaluated the PPS around the head before and after an echolocation detection task, in which the participants had to detect the presence of an object inside the peripersonal space by self-generated mouth clicks. To quantify the PPS, we adopted a behavioral measure, extensively used in previous studies (Canzoneri et al., 2012; Noel et al., 2015; Serino et al., 2015b; Teneggi et al., 2013), in which participants had to respond as fast as possible to a tactile stimulus applied to their body, while task-irrelevant sounds were presented, giving the impression of a looming sound. Previous results showed that sounds speeded up the detection of tactile stimuli specifically when presented at a certain distance from the participants (and not farther from them). Such distance can be measured as a proxy of the extent of the participant's PPS (Serino et al., 2015a, 2015b). In addition to the group that performed an echolocation detection task, the same PPS task was administered to two control groups of participants in order to directly link any change in PPS representation to echolocation and exclude general effects of increasing attention for an auditory stimulus at a given spatial location or task repetition. Thus, one control group performed the PPS task before and after a perceptual training, without any spatial component (auditory time bisection) and the other group took simply a break between the two sessions of the PPS task.

Participants

A total of 44 healthy sighted individuals were recruited to participate in this study (twenty-four females; average age 25.93, sd = ± 4.43). Participants have been assigned to 3 groups (see below). 16 participants were allocated to the echolocation group (ECHO) (2 participants were excluded from the analysis for their inability to complete the training); 14 participants to the temporal discrimination training (TIME) and 14 to the group who did not perform any task between the two PPS assessment (REST). All participants reported normal touch and hearing and gave written informed consent before starting the test. The study was approved by the ethics committee of the local health service (Comitato etico, ASL 3, Genova) and conducted in line with the Declaration of Helsinki

Procedure and apparatus

We started the procedure evaluating the PPS for all participants (Figure 3-**12**A), in order to assess the location of their PPS boundary before any training. The task was to respond as quickly as possible to a vibro-tactile stimulation on the neck, ignoring moving sound moving towards each participant. After, participants were divided into three groups: one experimental group (ECHO) and two control groups (TIME and REST). All participants were blindfolded during each task. Firstly we collected the data for the ECHO group, only after we recruited the other thirty participants for the TIME and REST group that was pseudo-randomly assigned to each group.

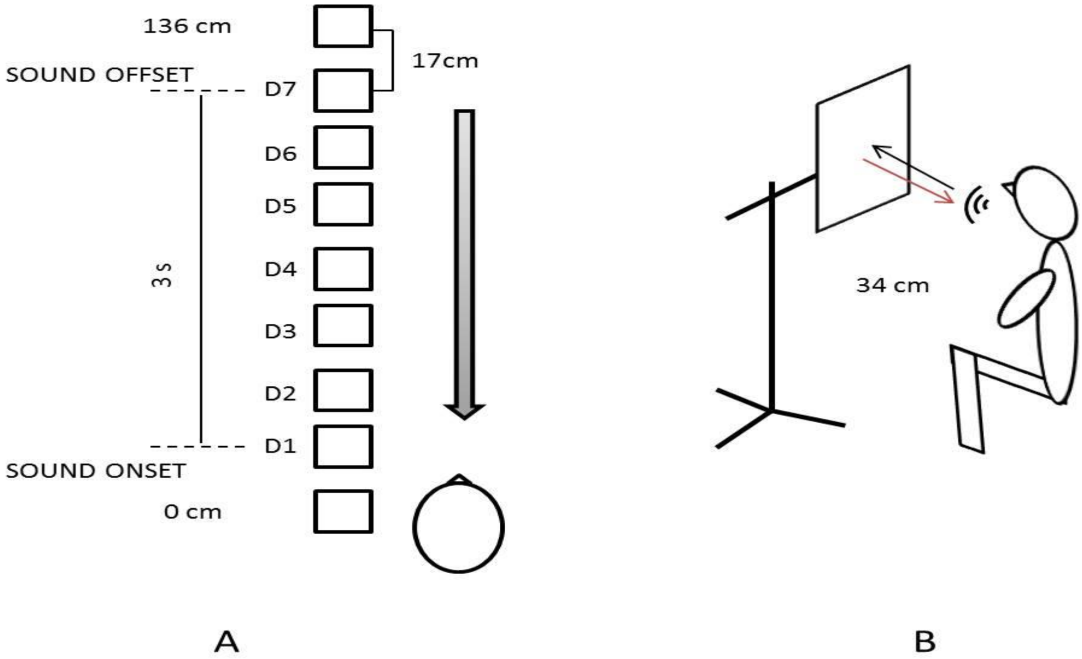


Figure 3-12. Experimental set-ups. (a) The set-up for the PPS task is shown. There were nine speakers generating sound sources at a different distance from the body. The first sound source was placed 17 cm apart from the left side of the head of each participant. The sound moved across the speakers as approaching the participant's head (grey arrow). The vibro-tactile device was placed on the left side of the neck. The tactile stimulus was delivered when the sound was placed at one of the seven possible depicted distances (17, 34, 51, 68, 85, 102, 119). (b) The set-up for the echolocation detection task is shown. We used a bar located at 34 cm ahead the participant. The black arrow and the red allow represent, respectively, It the path of the self-generated click and the echo reflected by the bar

The ECHO group (N = 14, 7 females) performed an echolocation detection task after the evaluation of the PPS. Participants were asked to sit in a different location from where the PPS task was performed so that the loudspeakers did not interfere with the echolocation task. During change position from the PPS setup to the other location, participants were allowed to remove the blindfold, but they did not see the object used for the task because it was previously hidden by view behind a cloth. We then selected naïve participants, before the beginning of the task, who received instructions on how to produce mouth-clicks to echolocate, after that they were blindfolded again. During the task, participants had to judge whether a bar of Plexiglas was in front of them or not, estimating the echoes produced by the mouth-clicks (Figure 3-12B). All participants first performed a training (10 trials), where they received a feedback on their responses, then 30 other trials without feedback.

The TIME (N = 14, 7 females) group performed an auditory time bisection task. The task consisted in hearing three sounds presented consecutively coming from the same source and judge which temporal interval is shorter: the one between the first and the second sounds or between the second and the third sound. In order to maintain the same procedure of the ECHO group, also the participants of this group were allowed to remove the blindfold for a few minutes and put it on again before beginning the time bisection task.

The third and last group, REST (N=14, 8 females), simply had 30 minutes of a break between the first and second assessments of PPS. They were allowed to remove the blindfold for just a couple of minutes. For the rest of the time, they kept the blindfold on.

All participants performed a second time the PPS task, in order to measure the changes in their PPS representation.

Moreover, all participants performed a control experiment to confirm that they were able to discriminate the different sound locations accordingly to the seven actual sound source positions (Canzoneri et al., 2012; Finisguerra et al., 2015).

Peripersonal task. The task of the participants was to respond as quickly as possible to a vibrotactile stimulation on the neck, ignoring moving sound moving towards him/her. For the acoustic stimuli, we used a custom-made device comprising an array of seven serial connected loudspeakers placed on a table on the left of the participant (figure 1a). The first loudspeaker was located at 17 cm from the head at its level and the last loudspeaker was at a distance of 119 cm. The distance between each loudspeaker was of 17 cm. The sounds (white noise) were originated from seven spatial sources so that the experimenter was able to precisely trigger the tactile stimulation when the sound was at the level of one of the loudspeakers located in space (Finisguerra et al., 2015). The sound moved along the distance of 102 cm in 3 s (i.e. at the speed of 34 cm/s). We sampled seven positions (17, 34, 51, 68, 85, 102 and 119 cm). For the tactile stimuli, we used a vibrotactile custom-made device consisting of a vibration motor. The motor had a surface area of 18 mm^2. The vibrotactile device was placed on the left side of participants neck. Tactile stimulation lasted 20 ms. The sound and tactile stimuli were controlled through a custom-made code running on Matlab© software.

The PPS task consisted of three types of trials, randomized among the experimental block (Canzoneri et al., 2012; Serino et al., 2015b). The critical trial for the task were experimental audio-tactile trials, approximately 60% of the trials, in which participants heard a sound and, at a given moment in time, received the vibrotactile stimulus, to which they were requested to respond saying ‘‘TAH’’ as quickly as possible, ignoring the auditory stimulus (Canzoneri et al., 2012). On each trial, the tactile stimulus was administered at one out of the seven temporal delays, which corresponded to a progressively shorter distance between the location of the sound and the body when the touch was given. Approximately 20% of the trial were unimodal tactile trials, whereby the target vibrotactile stimulus was delivered in the absence of auditory stimulation. Unimodal tactile trials were presented at two different temporal delays, corresponding to the equivalent time of the nearest (0 cm) and farthest distance (136 cm), so that when stimuli were presented there was no sound. Finally, approximately 20% of trials were caught trials, through which only auditory stimuli were presented and participants were requested to refrain responding. These trials were included in order to avoid an automatic response, to assure that participants were attentive to the task and to minimize an expectancy effect intrinsic in the task (i.e., participants become faster in responding as the trial goes by as they increase their expectancy to receive the tactile target (Kandula et al., 2017). Participants RTs were recorded by means of a microphone. Each participant performed a total of 140 trials, 28 unimodal tactile, 28 catch trials, and 12 trials for each audio-tactile combination. Inter-trial-interval was not fixed and each trial was started by the experimenter.

Echolocation detection task. The task consisted in detecting an object placed at about 34 cm from the head via the echo produced by emitted mouth clicks. A rectangular bar made of poly-methyl methacrylate (40 x 30 cm) was used as a target stimulus for the echolocation training. A staff held the bar with the longer side placed vertically (figure 1b). The bar was located in front of the participant at the head level. Participants performed the task, for a total of 40 trials. The first 10 trials (training block) were considered as training. On the other 30 trials (experimental block), the percentage of correct answers was calculated (for more details see below). The bar was presented in 50% of the trials. The participants had 20 s to give the response. To prevent participants from receiving any acoustic or floor vibration feedbacks due to moving the target, participants wore a pair of Philips SHL3000PP headphones, which played mixed music and the chair was located on a stack of rigid foam mats 4.5 cm high.

Auditory time bisection task. On each trial, participants heard three consecutive sounds and were requested to estimate which interval was shorter, the one between the first and the second sound or the one between the second and the third sound. The stimuli were 500 Hz tones, each having a duration of 75 ms. Sounds always came from the loudspeaker located at 34 cm from the head, i.e. at the same distance where the object for the echolocation task was placed. The experimenter took note of participants’ response at each trial. The interval duration between stimuli was determined by QUEST (Watson and Pelli, 1983), an adaptive algorithm which estimates the best stimulus value to be presented after each trial, given by the current participant's estimate. To ensure that a wide range of durations was sampled, the estimation was jittered by a random amount, drawn from a Gaussian distribution of time covering a range between 0 and 900 ms. The training included 80 trials. Inter-trial-interval was not fixed and each trial was started by the experimenter.

Control task. Each trial was identical to the bimodal trials of the PPS, but in this case, participants were asked to verbally indicate the perceived position of the sound in space when they had felt the vibrotactile stimulation, on a scale from 1 (very close) to 100 (very far) from the head. A total of 49 trials were performed, 7 for each position. The purpose of this task was to see whether participants were able to perceive the sound source at different locations according to their distance. It was performed by all participants.

Results

Before analyzing the data, we corrected bimodal RTs for the unimodal tactile RTs, used as a baseline, to eliminate a possible expectancy effect and subjects variability. To this aim, for each participant, we first identified the baseline condition resulting in the fastest RT among the unimodal tactile, and we used the mean of these two RTs. The mean of the unimodal RT for each condition was subtracted from the mean raw RTs of the bimodal stimulation for its relative condition (Noel et al., 2015; Salomon et al., 2017; Serino et al., 2015b).

ECHO We run three separated ANOVAs, one per group (Figure 3-**13**) with within factors Sound distance (17, 34, 51, 68, 85, 102 and 119) and Session (Pre, POST). As expected, the main effect of distance was significant for all the groups (ECHO, $F_{6,78} = 10.14$, $p = 2.87*10^{-8}$, $\eta^2 = 0.18$; TIME, $F_{6,78} = 11.53$, $p = 3.36*10^{-9}$, $\eta^2 = 0.11$; REST, $F_{6,78} = 6.29$, $p = 1.99*10^{-5}$, $\eta^2 = 0.06$). Instead, the main effect for Session was significant just for the group ECHO ($F_{1,13} = 7.86$, $p = 0.01$, $\eta^2 = 0.07$).

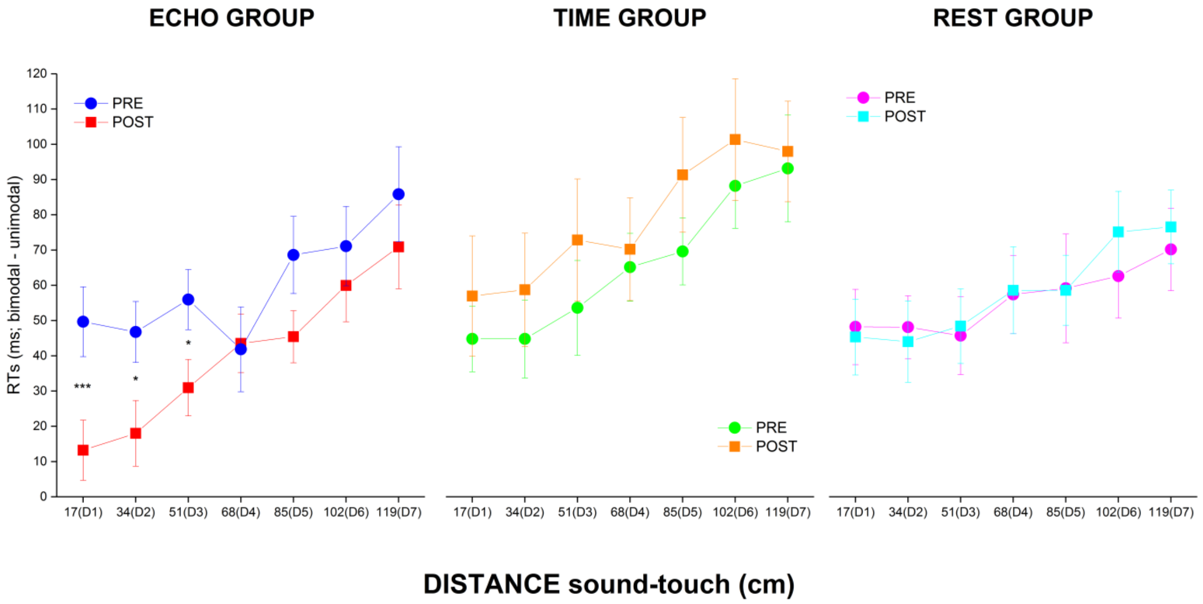


Figure 3-13. It shows the averaged bimodal RTs (normalized for the unimodal RTs) for each group, as a function of the seven distances sampled during the PPS task. Results for the ECHO group before (in blue) and after (in red) the echolocation training. Data for the TIME group before (in green) and after (in orange) the time bisection task. Data for the REST group before (in magenta) and after (in cyan) 15 minutes of break. (*) indicates a significant difference with $p < 0.05$. (***) indicates a significant difference with $p < 0.001$.

Also the two-way interaction Sound distance × Session was significant for the Group ECHO ($F_{6,78}$ = 2.49, p = 0.029, η^2 = 0.03) and not for the other two groups (Group TIME, $F_{6,78}$ = 0.43, p = 0.85, η^2 = 0.003; Group REST, $F_{6,84}$ = 0.60, p = 0.73, η^2 = 0.004).

Post hoc tests (with a Bonferroni correction for multiple comparisons) on the group ECHO (Figure 3-**13** on the left) revealed a significant reduction of corrected-RTs between POST and PRE sections for sound sources at 17 (t_{14} = -5.96, p = 0.0003), 34 (t_{14} = -3.42, p = 0.03) and 51 (t_{14} = -3.53, p 0.03). In order to control that the effect was due to a different on the unimodal RTs (Figure 3-**14**), used to correct the bimodal one, we run a 2-way Anova on the unimodal RTs; We had a within factor Session (PRE, POST) and a between factor Group (ECHO, REST and TIME). Results showed no significant effect for both the main factors (Session, $F_{1,39}$ = 2.9, p = 0.1; Group, $F_{2,39}$ = 2.08, p = 0.14) nor for the interaction ($F_{2,39}$ = 1.45, p = 0.24). Finally, in order to control possible differences between groups before the training, we conducted a 2-way Anova on the bimodal RTs obtain from the first repetition, with factor Group (ECHO, REST and TIME) and Sound distance. The main effect of distance was significant ($F_{6,234}$ = 11.05, p = 7.63×10^{-11}, η^2 = 0.1), whereas no main effect of Group ($F_{2,39}$ = 0.32, p = 0.7), nor a Sound Distance × Group interaction was found ($F_{12,234}$ = 1.09, p = 0.37). Results per the echolocation and time bisection task are reported in the supplemental materials. The percentage of correct responses of the echolocation task no chance level was 60,72% (sd = 10.39, t-test, t_{13} = 3.86, p < 0,002) significantly above the chance level(Figure 3-**15**).

Finally, we checked that participants did perceive the different sounds as coming from separate locations, using the control task. A repeated measure ANOVA run on participants' responses, with Distance as a within-subject factor, indicated a main effect of Distance ($F_{6,234}$= 305.61, p = 1.14×10^{-112}), indicating that, as expected, participants perceived sounds progressively closer to their body, as sounds approached. Data from

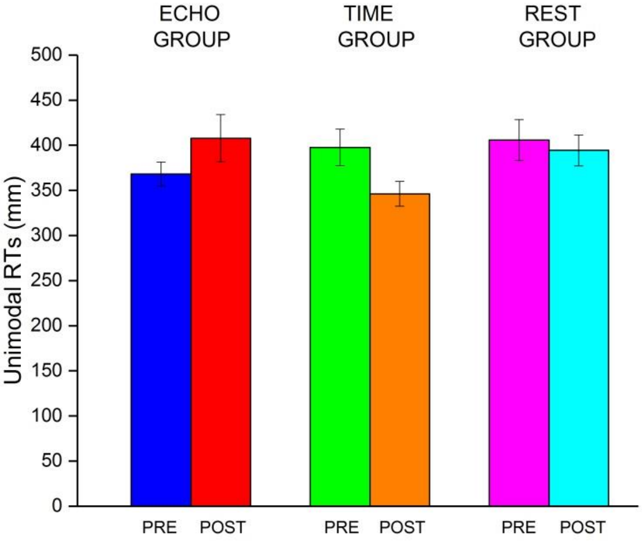


Figure 3-14. Bar plot represent the average RTs in the unimodal condition for each group before and after the auditory tasks in the Echo and Time group and for the first and second repetition in the Rest group.

confirmed that participants perceived the sound source at different locations according to their distance (Figure 3-**16**).

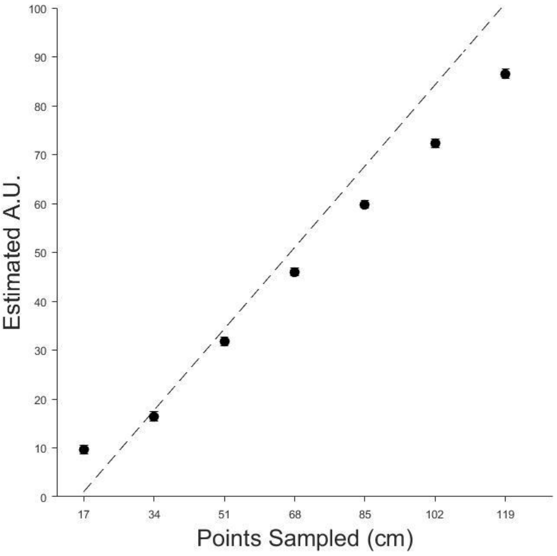


Figure 3-16. Estimate of sound distance as a function of point in space sampled for the 7-speaker setup. Participants estimated sound distance for sounds originating from 119 cm in front (positive x-value) and terminating at 17 cm at the head level.

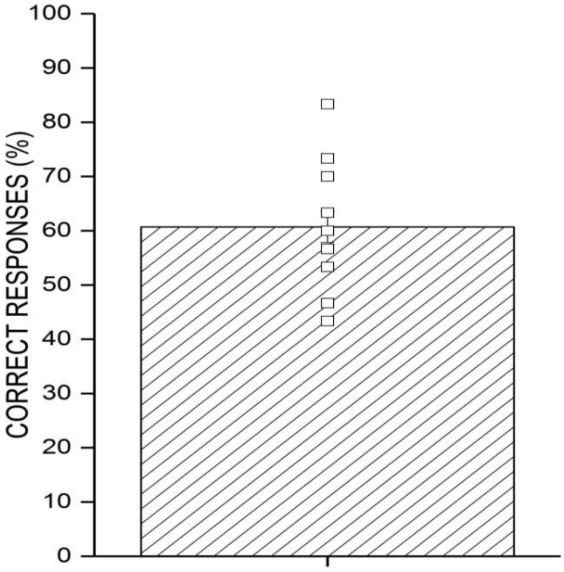


Figure 3-15. Percentage of correct responses in the echolocation task.

Conclusion

In the present study, we showed that performing an echolocation training, with stimuli presented in the near space, affected multisensory interaction within the space surrounding the body, named PPS. Results show that, after an echolocation task, consisting in detecting an external object presented at about 34 cm from the body via the echo produced by emitted mouth clicks, looming sounds interacted more strongly with the processing of tactile information on the body. In particular, after the training, the tactile RTs, around the area where the echolocation training was conducted, strongly speeded up compared to before the training, suggesting a change in the processing of the multisensory interaction within the PPS.

This effect could not depend on a learning process of the task used to evaluate the PPS, due to a simple learning through task repetition. Indeed, participants of the REST group, who were tested twice after the same amount of time as the ECHO group, did not show any change in their RTs between the first and the second PPS assessment. A more interesting account of the present effect might be that the change in multisensory interaction within the PPS found in the ECHO group was due to a general enhanced attention towards auditory stimuli in the near space. However, a shift of attention per se cannot explain the results of the ECHO group, because participants of TIME group, who were engaged in a demanding task on auditory stimuli occurring exactly at the same location as the echolocation training, did not show any specific changes in multisensory interaction after the training.

The main difference between the TIME and the ECHO group was in the nature of the task performed in the near space, which required analyzing, respectively, the temporal or the spatial feature of auditory cues. The present results suggest that only when the task required spatial processing, it produced a specific change in multisensory interaction. Furthermore, a second main difference between the two trainings was that the temporal training implied a perceptual task related to stimuli in the near space, whereas the echolocation task also implied a sensory-motor component, in which participants performed an action (i.e., emitting a sound with their mouth) and processed the sensory consequences of that action (the echo produced). We suggest that this second, sensory-motor, an aspect of the task is critical to determine its effect on multisensory processing. The sensory-motor spatial task implied in the echolocation training resembles tool-use: participants performed an action with a tool which allows them to extend their action possibilities in order to get sensory information from the far space. Previous studies showed that PPS can be modified by tool use training (Canzoneri et al., 2013; Holmes et al., 2007; Maravita and Iriki, 2004; Martel et al., 2016), whereas just displacing spatial attention towards the far space in order to point towards far objects (Canzoneri et al., 2013) or passively holding the tool (Farnè and Làdavas, 2000) is not sufficient for PPS extension. It might be argued that echolocation is more comparable to using a laser pointer or a flashlight that provides information about the distance of an object, but has no tactile consequences than to a tool. For example, an extension of PPS has been observed with a stick, physically connecting the body to extra-personal space, but not with a laser pointer (Berti and Frassinetti, 2000; Canzoneri et al., 2013). Recently, Serino et al. (2015) proposed a neural network model to explain plasticity in PPS representation induced by tool-use via multisensory congruency. They showed that the temporal congruency between a stimulus on the body and an auditory feedback from the far space drives the extension of multisensory integration towards the location of the sensory feedback. A similar mechanism can be suggested to explain the effect of the echolocation training: participants producing the clicks with the mouth performed a movement that produces a time coherent feedback between the tactile stimulation (mouth) and the echo from a further spatial location, during all process of detection. Our results suggest that the repetition for a given amount of time of such activity induces a specific effect on PPS processing for space where the training is performed.

In the present protocol, the object to be localized in the echolocation training was placed in a fixed position, near the participant. The present findings showed that the training did not induce actually an extension of the participants' PPS, because the reduction of the RTs was not found on all the positions sampled, but rather increased multisensory interaction around the location of the object (with a possible weaker effect for the origin of the echo generated by the room walls). This increase of multisensory processing in the near space might be seen as a difference as compared to previous reports about the classic extension of PPS induced by tool-use, as actually no PPS extension is shown in the present results. However, previous tool-use studies (Farne et al., 2005; Farnè et al., 2005, 2007) also showed that the change of PPS processing is specific for the location where the tool is functionally used, and thus it occurs at closer distances from the body in the functional part of the tool is there placed (see Gallivan et al., 2013; Magosso et al., 2010; Ursino et al., 2007 for a possible neural mechanism).

Echolocation is mainly used by blind people to locate objects in space or to navigate through the environment, in order to avoid obstacles. A similar function is achieved by blind people using the white cane. Interestingly, Serino et al. (2007) showed that a short training with a white cane is sufficient to temporarily modify PPS representation in sighted participants, whereas long-term blind cane users holding their cane show a PPS representation which is extended toward the tip of the cane, as if the cane constitutes the new boundary of their PPS (Witt et al., 2005). Such a remapping of PPS representation seem to have an adaptive value, i.e. allows to locate in advance a possible harmful object before it collides the body (Rossetti et al., 2015). Compared to the white cane, that physically allows reaching the far space, echolocation allows the blind to detect objects thanks to the interpretation of the echoes produced by the reflections of sounds. Therefore, we propose that echolocation is a way to reduce the lack of information about the space between the body and an external object in absence of visual cues. Increasing multisensory processing for that portion of space might be a key mechanism to achieve this function. Further investigation is needed to test whether echolocation can be compared to tool use in the far space producing an extension of PPS.

To conclude, in this work we have shown - for the first time, to the best of our knowledge - that the representation of PPS of the head can be modified by echolocation and that this effect is not related to a training effect, nor to a mere perceptual effect due to the presence of an acoustic sound source inside the PPS, but it likely depends on the congruency between a body action and a sensory feedback from a given position in space.

Chapter 4

General conclusion

The aim of this work is to clarify three points: 1) to investigate which is the role of the auditory system in spatial representation in sighted people and how vision and touch can *indirectly* influence auditory space perception. We used auditory spatial tasks to understand which are the environmental cues involved in the interaction between vision, audition, and touch in auditory spatial representation. 2) to study the role of vision in calibrating sensory systems, in particular, the auditory system in early blind individuals. In particular, we developed new tasks to assess specific aspects of spatial perception in order to identify spatial impairments 3) Understand some basic functions of human echolocation. Echolocation seems to help blind people to navigate and navigate in space and improve their spatial skills (Kolarik et al., 2017; Thaler, 2013; Vercillo et al., 2014). So the idea was to test whether spatial information can be acquired thanks to echolocation, when vision is not available, also in people that normally would acquire the same information through vision and see whether it is possible to train this ability.

4.1 Auditory spatial representation in blind and sighted individuals.

Until now, most of the research, that has focused on spatial cognition, has investigated how different senses interact with each other to create a homogeneous spatial representation of the external world (Burr and Alais, 2006; Ernst and Bülthoff, 2004; Newell et al., 2010). When it comes to spatial cognition, the visual system is considered the most accurate sense for space judgments and the most influential modality for cross-modal calibration of spatial perception during development (Gori et al., 2012). Many studies support this idea, showing that when there is an incongruence between the spatial locations of for example audio and visual stimuli, vision usually dominates, causing the so-called “ventriloquist effect” (Alais and Burr, 2004; Mateeff et al., 1985; Warren et al., 1981). During the ventriloquist effect, the auditory stimulus is “captured” by the visual system, making us perceived the sound in the same location of the visual stimulus. The ventriloquist effect has been explained as the result of optimal cue-combination where each cue is weighted according to its statistical reliability. Vision dominates the perceived location because it is more reliable then audition in spatial judgments (Alais and Burr, 2004).

In this work, instead of focusing on how vision and hearing interact directly with each other on spatial cognition, we have investigated the accuracy and precision of the sense of hearing in the spatial domain and which is the "*indirect*" influence of vision. We talk about "*indirect*" influence of vision because the tasks were purely acoustic and the role of vision is limited to spatial exploration before and after a task in the sighted subject, and the absence of it during development in early blind individuals.

In the first study presented (par. 2.1.1), we investigate the acoustic precision in blindfolded sighted participants in two auditory spatial tasks – MAA and spatial bisection. We tested their ability in two acoustically environments, normal room and an anechoic chamber, to see which is the contribution of the environments this kind of tasks. The interesting part was that participants had no previous knowledge of the structure of the room where the tasks were performed. We found an improvement of precision in the space bisection task but not in the MAA after the observation of a normal room. No improvement was found when performing the same task in an anechoic chamber. In addition, no difference was found between a condition of short environment observation and a condition of full vision during the whole experimental session.

In the second experiment (par. 2.1.2), we replicated the same experiment, but this time, instead of using visual exploration to create a mental representation of the environment, we allow to participants to haptically explore a 3D model of the room. This experiment was performed only in a reverberant room. What we found is that that haptic exploration, combined with vestibular feedback during navigation, increase precision in the space bisection task. The effect is not due to a learning process because the control group does not show the effect after the second repetition of the task without receiving any feedback about the structure of the room between the two repetitions.

From the first experiment, we can infer two things. The first is which are the environmental visual cues that are involved in auditory precision improvement, and second, why this improvement is present only in the reverberant room. Other studies before our have suggested that vision can interact with audition even when visual information is not informative for the auditory task, i.e. in the task are not presented visual stimuli (Jackson, 1953; Shelton and Searle, 1980; Tabry et al., 2013). In the reverberant room normally, the sounds, that are produced by the loudspeakers, are reflected by structural elements of the environment producing reverberation (echoes). This results in stimuli with scattering patterns or spectral coloration, or both, which are as much different as source locations are far apart. In the anechoic chamber do not happen because part of the sounds is absorbed by the walls, therefore the hearing system acquires almost exclusively the direct sound. Our hypothesis is that reverberation is an indirect source of information, triggered by vision. It is indirect because it cannot be accessed by pure listening: before observing the room, the room acoustics are somewhat 'hidden'. It is triggered by vision because precision increases after explicit knowledge of the room are acquired. Specifically, we interpret that in a normal room echoes add perceptual information to the direct path, that can be interpreted as noise and decrease the precision in performing the task, but not the accuracy because the sound source position remains clear. However, if it is allowed to the participant to create a mental representation of the room using landmarks obtained through vision, the auditory system is able to compensate for such mismatch produced by the noise and obtain performance comparable to those obtained in anechoic condition. For similar reasons, observing an anechoic room does not improve acoustic precision because visual knowledge of the room structure does not add extra information about acoustic cues that are absent: bluntly speaking, observing an anechoic room is 'spatially useless'. The same reasons applied to the results in the second experiment (par. 2.1.2), only that mental representation of space is created thanks to haptic exploration. Intuitively, it might be thought that the spatial information obtained by tactile exploration could not be sufficient to compensate for the mismatch produced by the noise because the amount of information is less than those obtained visually. We found that tactile information combined with vestibular feedback during navigation, are sufficient cues to create a mental representation of the space that helps to improve the understanding of room acoustics (Gori et al., 2014b). The similarity of results between vision and touch, it may suggest a supramodal acquisition of information (Campus et al., 2012; Leclerc et al., 2005).

These results could be useful for the development of possible rehabilitation techniques for blind people. As we discussed in chapter 1 and also later in this paragraph, some studies showed a deficit for some types of spatial tasks, that it may be due to a lack of calibration from the visual system in the early stages of development (Gori et al., 2014a). However, it remains to be verified whether this improvement, found thanks to tactile information, can also be obtained in blind people or requires a mature auditory system, which has been calibrated by a vision during development.

The second results found, especially in the first task, is that the improvement was found in the space bisection and not in the MAA. The reason behind it might be connected again with to the role of visual information on the calibration of the auditory system. The reason is intrinsic in the nature of the acoustic task. The MAA is a simple task in which the participant has to compare his own location with the location of the sound. In this case, the noise produced by the reverberation interferes only with the position of the sound and not with that of the body, so even if one of the two information about the location is not clean, the auditory system manages to maintain a good precision. The same thing does not happen for the space bisection, where all the information regarding the position of the sounds suffers from the interference produced by the reverberation, causing a decrease of precision. Therefore only a solid representation of the environment and the position of the set-up can lead to an improvement.

Concerning the auditory spatial ability of blind individuals, in literature, there are two lines of results. One line supports the "*Compensatory hypothesis* ", which theorizes that loss of vision is compensated by the intact sensory systems that are recruited to process spatial information and to develop an accurate sense of space (Collignon et al., 2009a; Collignon and De Volder, 2009; Hötting and Röder, 2009). Several studies found enhanced performance in discrimination of sounds pitch (Eschenbach, 2004; Gougoux et al., 2004), monaural localization (Doucet et al., 2005; Gougoux et al., 2004; Lessard et al., 1998; Röder et al., 1999) and relative distance discrimination (Kolarik et al., 2013; Voss et al., 2004). On the other side, there is the "*General loss hypothesis*", which argues that vision is the only sense to encode spatial information, therefore the lack of vision does not allow blind individuals to develop a correct spatial representation (Eimer, 2004). Congenitally blind individuals are not able to perform specific auditory tasks, such as the space bisection (Gori et al., 2014a; Vercillo et al., 2016), reproduction of moving sounds (Finocchietti et al., 2015), vertical localization (Lewald, 2002; Voss et al., 2015; Zwiers et al., 2001) and distance discrimination (Cappagli et al., 2015; Kolarik et al., 2013).

Gori et al. (2014a) had put forward a hypothesis in between these two main lines. Starting from the fact that vision is the main sense to estimate spatial information, the idea is that during early development vision calibrates other senses to process spatial information. Lack of vision in the early stages of development may lead to spatial impairment for some aspects of spatial representation, that require a more complex understanding of space, both from a quantitative and a qualitative point of view. These amount of information can be obtained only by vision. At the same time other simpler aspect of spatial information, that do not require visual calibrations, are maintained showing the enhanced performance of blind people.

This hypothesis is in line with the results presented in paragraph 2.1 in which has been proven that visual information seems to be important also during adulthood to improve precision in the auditory spatial task in normal conditions (reverberant room). Moreover, studies regarding multisensory integration during development found that integration among senses does not take place before 8-10 years of age based on the complexity of the task (Adams, 2016; Ernst, 2008; Gori et al., 2008, 2010, 2012; Nardini et al., 2008; Röder et al., 2013), and that when children have to judge spatial information are influenced by visual stimuli (Gori et al., 2012).

Despite all these insights about the role of visual experience in shaping spatial representation, all the features under which enhancements or deficits of spatial perception occur in blind people have not been yet identified. The studies presented in paragraph 1.2 were made to try to give an explanation about these conflicting results.
Results of both studies in paragraph 2.2 showed how an early blind individual is not able to perform tasks in which is required to discriminate spatial relations between sounds and when are involved head movement during auditory localization. On the contrary, they exhibited fine performance, as sighted people or even better, when the relation has to be made between the auditory targets and the location of their own body. All these tasks have been developed to create a dissociation between the allocentric and egocentric frame of reference and to test the ability of early blind individuals to switch between one reference to the other based on the task. Clearly, our results showed an impairment of blind people to use an allocentric frame of reference.

It has been suggested that the acquisition of an allocentric frame of reference requires visual experience since several studies showed that in absence of vision individuals primarily rely on egocentric frames of reference to carry out spatial tasks (Cattaneo et al., 2008; Coluccia et al., 2009; Corazzini et al., 2010; Millar, 1994; Pasqualotto and Proulx, 2012) and to create a mental representation of space. For example, Corazzini at al. (2010) tested the ability of blind people and blindfolded controls to develop knowledge of an environment with the support of simultaneous auditory cues to find a target using the allocentric or egocentric frame of reference. They found that blind people spontaneously maintain to rely on an egocentric spatial representation, even when it was not favorable for performing the task.

On the contrary, auditory external frame of reference in sighted people is anchored to visual information (Foley et al., 2015), because the external representation seems to come from the spatial alignment between sensory modalities in eye-centered coordinates (Cohen and Andersen, 2002; Jay and Sparks, 1987; Pouget et al., 2002). It might be that even if blind people can benefit from external acoustic landmarks, the spatial remapping from egocentric to allocentric coordinates doesn't occur because audio-visual integration is not possible. Moreover, auditory spatial information cannot be compared with the amount of information that can be acquired exploring the space with vision, in terms of acuity, the spatial relationship between body position and external objects (especially if silent), but above all, the spatial relationships among external objects.

Other psychophysical studies examined the role of vision played in the formation of the spatial representation of tactile localization demonstrating that an early blindness prevents the automatic remapping of touch into external space (Crollen et al., 2017a; Röder et al., 2004). For example, when the performance of blind and sighted participants is compared in a Temporal order judgment task (TOJ) with hands crossed over the body midline, sighted but not blind participants hesitated, revealing an internal conflict between body-centered and external frames of reference. The fact that there was no difference between bind participants performance was related to an altered activation of the parieto-frontal network normally involved in the coordinated transformation process (Crollen et al., 2017b), suggesting that the integration of body-centered and external frames of reference for touch localization might be driven by developmental vision. On the other hand, early blind individuals can coordinate bimanual movements using externally-based spatial principles like the sighted, suggesting that reference frames are applied flexibly depending on task demands (Badde et al., 2014; Crollen et al., 2017a). It seems that visual loss does not bleach completely the integration of body-centered and externally defined reference frames but rather appears to differentially affect the automatic weight attributed to each frame of reference depending on task-specific spatial requirements. It might be that the tasks to which the blind participants were subjected require a strong use of external reference landmarks that can only be acquired thanks to a mature spatial representation system.

To conclude, in this first part we have shown that auditory spatial cognition is influenced by visual experience during development because people with early blindness are not able to estimate correctly spatial information. Also in adults, with a correct development of the visual system, the visual experience (and also tactile) is important, because when it is not possible to create an a priori mental representation of the environment, participants were affected by the acoustics of the environment decreasing their precision in complex spatial tasks.

All these results lead us to introduce the second topic dealt with in this work that is human echolocation, that will be discussed in the next paragraph.

4.2 Echolocation and spatial representation

Echolocation can be considered as the connection between audio-spatial and visuospatial information and an alternative way to provide spatial information and a good substitute for vision allowing a self-calibration of the auditory system in congenitally blind individuals.
A recent study (Vercillo et al., 2014) has compared the performance of blind expert echolocators, blind and sighted people, these last two groups with no previous experience of echolocation, in a complex space auditory task. It was found that, contrarily to blind nonexpert echolocators, blind expert echolocators performed the spatial task with similar or even better precision and accuracy than the sighted group. This supports the hypothesis that echolocation recalibrates and even refines the ability of blind individuals to represent sounds in complex spatial configurations and compensate the lack of vision. Moreover, it seems that developing the ability to echolocate can offer real-life advantages for blind people, fostering social inclusion: echolocation is associated with higher salary and mobility in unfamiliar places, providing evidence that echolocation may play a role in successful adaptation to vision loss (Thaler, 2013).

This is the reasons why, in chapter 3, we focused on investigate some basic functions of human echolocation. Mainly we wanted to see how fast it is possible to learn echolocation. For this reason in the first experiment (par. 3.1), we developed an echolocation depth task, in which participant had to judge the position in depth of real objects. They have undergone a training and after tested in experimental condition to see whether the training had an effect. Furthermore, in the same experiment, we tested which is the contribution of environmental cues and the kind of technique used to produce the echolocation signals. Therefore we performed the experiment in two different rooms - anechoic chamber and reverberant room – and allow participants to use finger snaps or mouth clicks. In the second experiment (part 3.2), we wanted to test the ability of novice sighted participants with a more ecological setup. We built an L-shaped corridor and asked blindfolded participants to walk along it and to orientate themselves to understand how the corridor ended, only using echolocation with self-generated clicks. Other than evaluating the percentage of correct responses, we evaluated the kinematics of movements of the head and the body, using a motion capture system, to see whether there was a correlation with the response. These results could be the basis of a model of movement to teach to improve the ability to echolocate during, for example, a rehabilitative program.

In the first experiment (par. 3.1), we found that sighted people are able to perform a depth echolocation task after just around one hour of training in line with previous studies that investigated learning skills in sighted individuals (Rosenblum et al., 2010; Schenkman and Nilsson, 2010; Teng, 2011; Thaler et al., 2014b). Thanks to the training there is a general improvement in the performance, participant more precise and accurate. One thing to highlight is the great variability in performance among the participants even in the last experimental session. It has been little discussed in the literature the reason why is present this variability. It has been proposed that it can be related with the vividness of visual imagery in sighted people because it has been found a positive correlation with the ability to echolocate (Thaler et al., 2014b). Moreover, it was found a positive correlation between the improvement in echolocation and sustained and divided attention, as measured in the Paced Auditory Serial Attention Task (Ekkel et al., 2016).

Another result was obtained comparing the performance in the anechoic and reverberant room. We found that there is no difference in the percentage of correct responses, but, the interesting point is that in the reverberant room participants are more accurate and precise compared to the group that performed the task in the anechoic chamber. This is a crucial point because the majority of experiment about echolocation were performed in anechoic or damped rooms (Milne, Anello, Goodale, & Thaler, 2015; Teng & Whitney, 2011; Thaler, Wilson, et al., 2014) and understand if there is a difference in performance can help for future studies. A possible explanation is that the reverberant room provides more cues comparing the anechoic chamber, i.e. the reverberation per se. While in the anechoic chamber there is just one set of information to localize the silent object, i.e. the direct path of the echoes (early reflections) that is the reflection of the sound on the object, in the reverberant room there is also a second set of echoes, the ones produced by the sound reflecting on the walls (late reflections). All the echoes together change based on the location of the object, suggesting that some acoustical characteristics, such as late echoes and spectral coloration of the reverberant room, can be as important as the early echoes, which are known to be interpreted by our brain in terms of binaural cues (Libbey and Rogers, 2004; Shinn-Cunningham et al., 2005). The binaural cues, however, in our setup, are arguably not mainly responsible for the difference between the two rooms, because the reflecting objects are located in front of the participant. When objects are facing the participant, the time lag between the right and left ear (Interaural Time Difference) of the main reflected sound is almost zero. As well, the difference in sound intensity impacting the ears (Interaural Level Difference) is almost zero. Finally, the energy of the direct path does not approximately depend on distance, since we imposed acoustic size constancy, therefore it may not have modulated our results. That is, the information from the direct path in both environments in this study is small. Therefore, information must have come from all that was left: the difference we observe the two environments can be ascribed to late echoes, to the mixed binaural cues that they elicit when sound bounce in every direction (therefore not in front of the participant) and to the possibly different spectral coloration cues that these echoes, together, cause when putting the objects at various distances. Finally, we found that there is not a significant difference between the two techniques used to produce the clicks – mouth click and finger snaps. From these results we can infer that probably the manner in which the sound is produced by novice echolocators does not matter in a depth task, but rather the amount of available environmental cues is the key factor (i.e. room reverberation).

In the second experiment (par. 3.2) we added a missing other studies that had investigated navigation by means of echolocation (Kolarik et al., 2016, 2017), because instead of limiting the study to quantify movement variables, such as speed, distance of the target etc., we wanted to see which was the relationship between these variables and the response. We identify three main factors the might influence the echolocation performance: time, space and head motion. We did not find an influence of completion time in the number of correct responses, that is fast body motion seems not related to a better understanding of an unknown environment. A similar result appears when evaluating travel aids such as white canes, that on one hand reduce collisions but do not necessarily decrease task completion time (Kim and Cho, 2013). As well, completion time seems the weakest predictor of performance when both blind and visually impaired persons get explicit feedback on spatial properties of unknown paths (Kalia et al., 2010). The second point is space, we found a significant link between the spontaneous stop point and the probability of correct guessing, with people stopping earlier as more reliable predictors of the corridor shape. Therefore, an external observer (for example a rehabilitation practitioner) may infer whether a blindfolded person has well understood the environment by only looking at where decisions are taken, no matter the response. About head movement, the utility of head movements during an echolocation task had already been demonstrated (Milne et al., 2014b; Wallmeier, L ; Wiegrebe, 2014),what our results add is that the influence of head motion seems not to be biased by some sort of lateralization dependent on the setup and that active head exploration seems, therefore, necessary to understand structural properties from echolocation.
All these results may serve as a guideline for orientation and mobility practitioners and in general to gain knowledge about the link between the behavior of persons in the dark and their understanding of where they are.

The third experiment about echolocation (par 3.3) does not directly test the ability to echolocate, but rather how echolocation can influence multisensory integration in a spatial task. So one might think that an echolocation training can lead to a greater integration of information. We tested this hypothesis measuring participants' reaction times to a tactile stimulation, while task-irrelevant looming auditory stimuli were presented, in a task used to evaluate peripersonal space (PPS). We showed that performing an echolocation training, with stimuli presented in the near space, affected multisensory interaction within the space surrounding the body, while this improvement was not found with a training based on time. The present results suggest that only when the task required spatial processing, it produced a specific change in multisensory interaction. Furthermore, a second main difference between the two trainings was that the temporal training implied a perceptual task related to stimuli in the near space, whereas the echolocation task also implied a sensory-motor component, in which participants performed an action (i.e., emitting a sound with their mouth) and processed the sensory consequences of that action (the echo produced). We suggest that this second, sensory-motor, an aspect of the task is critical to determine its effect on multisensory processing. The sensory-motor spatial task implied in the echolocation training resembles tool-use: participants performed an action with a tool which allows them to extend their action possibilities in order to get sensory information from the far space. we propose that echolocation is a way to reduce the lack of information about the space between the body and an external object in absence of visual cues. Increasing multisensory processing for that portion of space might be a key mechanism to achieve this function.

To conclude, our results show how spatial representation is dynamic and adaptable to both short and long-term contexts. In addition, we believe it is important to focus on the study of echolocation, in particular with a view to a rehabilitation process based on echolocation, since it seems to bring a lot of benefit to blind individuals that use it in daily life (Thaler, 2013). The rehabilitation could be combined with a new technology to facilitate learning of echolocation for children and adults with visual disability, to improve their mobility and their ability to orient themselves

From our studies, we can state first that this new technology should use natural, ecological and personalized sounds (i.e. audible sounds that are informative about the environment, that humans can choose and produce by themselves), without coding the space with artificial sensory inputs. Second, it should be used as a rehabilitative tool facilitating learning and only for a limited period of time. Instead of *substituting* vision, it would be more useful if it facilitated natural echolocation as a way to regain functionality lost through blindness.

List of Figures

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