University of Genova and
Istituto Italiano di Tecnologia

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From sensory perception to spatial cognition.

by

Elena Aggius-Vella

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Dr. Monica Gori   Supervisor
Name   Head of the PhD program

Dibris

Department of Informatics, Bioengineering, Robotics and Systems Engineering

I would like to dedicate this thesis to my grandfather Enrico Marchi …

Declaration

I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other university. This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and Acknowledgements. This dissertation contains fewer than 65,000 words including appendices, bibliography, footnotes, tables and equations and has fewer than 150 figures.

Elena Aggius-Vella
February 2019

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Writing the doctoral thesis was a very satisfying job, because it summarizes and provides an overview of the work done in these three years. The choice to study the brain has certainly been influenced by past events and has been made possible thanks to the help of many people around me.

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Abstract

To interact with the environmet, it is crucial to have a clear space representation. Several findings have shown that the space around our body is split in several portions, which are differentially coded by the brain. Evidences of such subdivision have been reported by studies on people affected by neglect, on space near (peripersonal) and far (extrapersonal) to the body position and considering space around specific different portion of the body. Moreover, recent studies showed that sensory modalities are at the base of important cognitive skills. However, it is still unclear if each sensory modality has a different role in the development of cognitive skills in the several portions of space around the body. Recent works showed that the visual modality is crucial for the development of spatial representation.

This idea is supported by studies on blind individuals showing that visual information is fundamental for the development of auditory spatial representation. For example, blind individuals are not able to perform the spatial bisection task, a task that requires to build an auditory spatial metric, a skill that sighted children acquire around 6 years of age.

Based these prior researches, we hypothesize that if different sensory modalities have a role on the devlopment of different cognitive skills, then we should be able to find a clear correlation between availability of the sensory modality and the cognitive skill associated. In particular we hypothesize that the visual information is crucial for the development of auditory space represnetation; if this is true, we should find different spatial skill between front and back spaces.

In this thesis, I provide evidences that spaces around our body are differently influenced by sensory modalities. Our results suggest that visual input have a pivotal role in the development of auditory spatial representation and that this applies only to the frontal space. Indeed sighted people are less accurated in spatial task only in space where vision is not present (i.e. the back), while blind people show no differences between front and back spaces. On the other hand, people tend to report sounds in the back space, suggesting that the role of hearing in allertness could be more important in the back than frontal spaces. Finally, we show that natural training, stressing the integration of audio motor stimuli, can restore spatial cognition, opening new possibility for rehabilitation programs. Spatial cognition is a well studied topic.

However, we think our findings fill the gap regarding how the different availibility of sensory information, across spaces, causes the development of different cognitive skills in these spaces. This work is the starting point to understand the strategies that the brain adopts to maximize its resources by processing, in the more efficient way, as much information as possible.

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Chapter 1

Introduction

It is known that the brain has a limited amount of cognitive resources to spend at the same time. However, we are continuously stimulated by thousands of different sensory information caming from everywhere.It is still unknown if and how the brain is organized in order to be able to process as many stimuli as possible coming from every portion of space. The aim of this work is to understand how different sensory modalities and the movement of different limbs affect cognitive skills in the several portions of space surrounding the body. This work is the starting point to understand the strategies that the brain adopts to maximize its resources by processing, in the more efficient way, as much information as possible. .

1.1 Spatial representation around the body: is there one or more?

It has been found that the representation of space around one's body is split in several regions based on anatomical and neural activities. This evidence comes from the electrophysiological works, reported by di Pellegrino and Làdavas (2015), studies on unilateral spatial neglect patients Farnè and Làdavas (2002a); Saj and Vuilleumier (2007); Vallar et al. (1995); Viaud-Delmon et al. (2007), and studies on the peripersonal space by Aimola et al. (2012); Cléry et al. (2015); Rizzolatti et al. (1997); Serino et al. (2015). These sections of space seem to be differentiated based on their relationship to one's body position. For additional details regarding what is known about these different representations please refer to Ladavas and Serino (2008) regarding near and far spaces, Occelli et al. (2011); Saj and Vuilleumier (2007); Viaud-Delmon et al. (2007); Zampini et al. (2007) regarding frontal and rear space, di Pellegrino and Làdavas (2015); Serino et al. (2015) regarding the spaces around specific parts of the body and Finocchietti et al. (2015) results regarding the spaces above and below the head in the frontal field. Spatial representation can be split in several different representations with respect to one's basic body structure: front vs back, far vs near, and upper body vs lower body. Each of these regions can be differently modulated by the available sensory modalities and the possible body movement in each space (i.e. vision and movement in frontal space, hearing everywhere). Additionally, it has been showed that different neural networks contribute to different spatial representations depending on the attentional processes. The division between the peripersonal and extrapersonal spaces is the most well understood currently. The peripersonal space (PPS) is defined as the space immediately surrounding the body Rizzolatti et al. (1997). This is the space within which we can grasp and manipulate objects. By contrast, extrapersonal space refers to the space beyond one's grasping distance. The active exploration of this space is limited to eye movements. The reason of the existence of a functional difference between the PPS and extrapersonal space remains unclear. Two current hypotheses not mutually exclusive (see Brozzoli et al. (2014); di Pellegrino and Làdavas (2015))have been proposed. The first suggest that the role of the PPS representations may primarily support goal directed, actions directed toward objects Rizzolatti et al. (1997, 1981). The second hypothesis views the PPS as a defensive space, where stimuli are more quickly detected, which arouses quicker defensive reactions to avoid close threats de Vignemont and Iannetti (2015); Graziano and Botvinick (2002); Sambo et al. (2012) proposed that these two functions of peripersonal space would require distinct sensory and motor processes which would obey different principles. To support this view, they showed that anxiety and tool use differently affect the representation of one's peripersonal space. Anxiety reduces the extension of the working space while extending protective space. While, tool use extends the working space but has no effect on protective space. The peripersonal space is represented through multisensory coding and its neural correlates are located in the parietal and frontal premotor cortices, which are also crucial for the control of somatic, head and arm movements Gentilucci et al. (1983); Graziano and Gross (1998); Hyvarinen and Poranen (1974); Rizzolatti et al. (1981). In this cortical area (especially in area F4), a large proportion of neurons are bimodal and both tactile and visual stimuli can active them. The differentiation between these peripersonal and extra personal spaces is due to the activity of neurons F4. These neurons respond poorly to stimuli far from the body, however they respond well to objects moving near the body (peripersonal) space Gentilucci et al. (1988, 1983); Rizzolatti et al. (1981). Some F4 neurons respond only to stimuli very close to the body surface, while others can be triggered by stimuli located further away, but still within the reaching distance (e.g. distant peripersonal neurons). Interestingly, Graziano et al. (1999) showed that F4 neurons integrate not only tactile and visual information but also auditory information about the location of objects within PPS, suggesting that premotor area F4 build a multimodal representation of nearby space. Moreover, F4 neurons appear to code the location of a visual stimulus with respect to the face, arm, hand, or other body parts, leading to further parceling of space around specific part of the body. The putamen is another spatial area, showing neural activity during the representation of the space near the body Graziano and Gross (1993, 1995). Similarly, to the bimodal neurons in F4, the visual and tactile RFs in the putamen are spatially aligned, with the visual RFs being associated to the tactile ones. In this way, bimodal cells with tactile RFs on the arm respond visually when the arm is within the field of view but do not respond when the arm is moved out of view Gross and Graziano (1995). RFs of neurons in the regions processing PPS are not static, but rather dynamic, easily modified and shaped by sensorimotor experience Fogassi et al. (1996). Data supporting discrete brain representations of the space near the body and its parts comes from animals studies and patients with disorders of spatial attention, specifically patients presenting with contralesional extinction (single stimuli presented to either side are detected while when the same stimuli are presented to both sides simultaneously, the stimulus on the contralesional side is typically missed) Bender (1952). Controlesional extinction may be found between concurrent stimuli in the same sensory modalities (i.e. unimodal extinction), and between stimuli in different modalities (i.e. crossmodal extinction) Làdavas and Pavani (1998); Pellegrino et al. (1997) found that crossmodal, visual–tactile extinction only arises if visual stimuli are presented in the space near the ipsilesional, right hand and not when visual stimuli are far from the hand. Interesting, a study Farnè et al. (2005) revealed that PPS is organized in a modular fashion, meaning that the space near the body is split into distinct body parts, and processed differently by the brain. This parcelling was well investigated by Serino et al. (2015) who found that the size of PPS varied according to the part of the body stimulated. These different spatial portions differed in size, being progressively bigger for the hand, then face, and largest for the trunk. Finally, the extension of PPS around the hand and the face varied according to their relative positioning and stimuli congruency, whereas the PPS of the trunk was constant. These results suggest the existence of three PPS representations that are specific to different regions of the body and differ in extension and directional tuning. These distinct PPS representations, however, are not fully independent from each other, but referenced to the common reference frame of the trunk. The body part-centered PPS representations provide an effective mechanism to guide actions directed at objects within reaching distance using different effectors.

A second important division is between the front and back spaces. These two spaces differ in what sensory feedback is available. In the frontal space, both motor and visual feedbacks are available which leads to a good spatial representation. While, in the back space, only auditory information is available for detecting and localizing stimuli. Body movement is limited in the back space. Due to these differences in sensory input, different spatial representations could be developed during childhood. It is still matter of debated, whether, and to what extent, multisensory interactions is modulated by the spatial features of the stimuli. Differences in representation and perception between front and back spaces have been found in several studies involving different tasks and population. Some of these works showed spatial stimuli features differ in their importance to multisensory integration of stimuli delivered in the back or frontal space. It could be suggested that this differentiation is due to the different characteristics of sensory modalities available in the two spaces, as show in the following studies. Occelli et al. (2010) found a significant audiotactile Colavita effect (i.e, when reporting on the visual component of pairs of audiovisual or visuotactile stimuli during speeded detection vs discrimination task preferentially). Specifically, when stimuli were presented on the same (vs. opposite) side this effect only occurred in the back space and not when stimuli were presented in frontal space. This result can be explained by considering that the spatial factors differentially affect audiotactile interactions as a function of the region of space in which they occured. Studies on multisensory integration support this interpretation. Spence et al. (2003); Zampini et al. (2003a,b) investigated multisensory interaction, involving auditory and tactile stimuli, delivered in the front and back spaces. They found that the integration of stimuli in frontal space tend to be less sensitive to spatial manipulations than sensory interactions involving vision as one of the component modalities Spence et al. (2003); Zampini et al. (2003a,b). By contrast, the processing of the auditory and tactile spatial cues can be improved by presenting the stimuli in the portion of space where visual cues are typically not available Kitagawa et al. (2005). This data suggests that vision has a pivotal role in spatial localization. Interestingly, the improvements in performance in detecting/discriminating audiotactile stimuli, occuring when information is presented from different locations, is selectively observed in those conditions in which stimulation occurs in the rear space. This suggests that spatial representation in the rear space is weaker refined/less precise than in the frontal space. In other words, which spatial domain is less important for integrating stimuli in the back than in other regions. This pattern of results strengthens the hypothesis that when the portion of space behind the head is stimulated, the interactions between auditory complex stimuli and tactile stimuli are more pronounced than when stimuli are presented in the frontal space. Of particular interest, is that in the present context, the spatial arrangement of the stimuli and, in particular, the portion of space from which the stimuli were presented, have been shown to play a profound role in modulating audiotactile interactions. Farnè and Làdavas (2002a) tested patients with neglect who were presenting with extinction. Crossmodal audio-tactile extinction was more severe when assessed in the back space of the patients (where vision is not available), in comparison to the front space (where vision is usually available), which suggests that different degrees of multisensory integration may occur depending upon the functional relevance of a given modality for that particular sector of space. This pattern of results are more prominent with complex sounds, whereas pure tones induce only a mild form of crossmodal extinction. In particular, while white noise bursts exerted a stronger influence on tactile processing when the sounds were presented in the rear (vs. front) space, the milder effects induced by pure tones were selectively observed in the rear space but not in the frontal space. This is particularly interesting given that the spectrally dense auditory stimuli (i.e. stimuli that contained a wide range of frequencies) allow for a more precise encoding of interaural time differences (see Middlebrooks and Green (1991) for a review), thus causing noticeable improvements in auditory localization for white noise bursts but not for pure tones (e.g.,Occelli et al. (2009). The different effects between the two kinds of sounds in the two spaces suggest that 1)spatial location of stimuli in the back is not so relevant for detecting stimuli (as poor sound are not well localized) and 2)sound stimuli in the back have a special saliency (as both kind of sounds produced extinction).

Usually crossmodal auditory-tactile extinction observations show that sounds strongly interfere with the processing of tactile inputs when they were presented further from close to the head (i.e., at a distance of 20 cm), but the effect was substantially reduced when they were presented far from the head (i.e., at a distance of 70 cm). Crucially the results obtained by Farnè and Làdavas (2002a) were not modulated by the distance from which the sounds were presented Kitagawa et al. (2005) supporting the privileged role of hearing in the rear space. These finding collectively suggest that auditory stimuli have a different impact on attention depending from their spatial location (front vs back spaces). This could be explained by the fact that, while hearing is the only sense able to detect stimuli in the back space, it is possible that it has a privileged role (easier/faster activation of arousal) than in the frontal space, where vision is usually employed. Other evidences showing differentiation between front and back comes from lesion studies Viaud-Delmon et al. (2007), that showed that a lesion in the posterior parietal cortex, involved in planning movements, selectively affects the spatial representation only of the space toward which the actions can be directed (i.e. the frontal space), and not in the rear space where little movement is possible. Another study Kóbor et al.

(2006) investigated whether professional piano players and non-musicians differed in their ability to appropriately reconstruct the spatiotemporal order of a series of multiple tactile stimuli, when presented in the frontal space versus back space. Even though tactile temporal order judgments were significantly better in the musicians, overall both groups showed a significantly reduced crossed-hands deficit when their hands were crossed behind their backs rather than at the front. These results suggest that the spatiotemporal representation of non-visual stimuli in front versus rear space is different and this can be related to differences in the availability of visual input. All these studies lead to the conclusion that the presence of vision influences multisensory integration as well as spatial representation. This is further supported by Kóbor et al. (2006); Vallar et al. (1995)'s work which assessed subjective location of the mid-sagital plane during a free-field auditory localization task in the front and in the back half-spaces in right brain-damaged patients with spatial hemineglect and right brain-damaged patients without spatial hemineglect, and normal control subjects. The results of these studies suggest that patients with hemineglect report the subjective mid-sagittal plane displaced rightwards in both half-spaces. Both patients without hemineglect and controls, in contrast, made minor errors, and showed a greater displacement towards the left side in the back half-space. In four right brain-damaged patients, the rightward displacement was confined either to the front, or to the back half-space. These results further support the current thinking about the parcelization of space around us, and the possibility of different neuropsychological representation of front versus back space. The third proposed special division is in the vertical domain, specifically difference in how humans represent and process information in the upper vs lower body space. Adair et al. (1995) reported a single case study of a patient with bilateral signal abnormality within the inferior occipital and temporal regions. The patient showed neglect for stimuli in the superior vertical and far radial space. By contrast, other accounts of patients with neglect of radial and vertical space suggest that injury to parieto-occipital regions comprising the dorsal visual pathway produced neglect for inferior vertical and near radial space Butter et al. (1989); Rapcsak et al. (1988). Spatial neglect is thus thought to impede perception and exploration of space along multiple spatial axes. In another work, Butter et al. (1989) studied a patient after a traumatic brain injury. The patient showed extinction to a visual stimulus presented in the lower field when another stimulus was simultaneously presented in the upper field. When estimating the midpoint of vertically-oriented rods presented below eye level using visual cues, tactile/kinesthetic cues or a combination of these cues, the female patient consistently pointed higher than control subjects did. She showed less severe impairments on this task when the rods were presented at or above eye level. When estimating the midpoint between auditory clicks presented above and below her head, she pointed higher than did control subjects. These deficits cannot be accounted for by sensory or motor disorders and appear to be due to a disorder in attending to stimuli in the lower half of space. Rapcsak et al. (1988) reported a patient demonstrating altitudinal neglect who had Balint's syndrome caused by bilateral parieto-occipital infarctions. On visual and tactile bisection tasks using vertical rods, the patient consistently placed her mark well above the true midpoint; this performance remained unchanged when the stimuli were simultaneously explored visually and tactually. She also showed altitudinal inattention in the visual modality by extinguishing the stimulus presented in the lower quadrants during simultaneous paired stimulation across the horizontal meridian. These findings suggest that the parietal lobes are necessary for multimodal attentional and exploratory behaviors along the vertical dimensions of extrapersonal space. Until now, the majority of the studies, investigating spatial perception, focused their attention on the space around the upper part of the body (as reported above), while space around legs has been studied less. However, there are few studies on PPS showed similar results looking at performance on tasks judging stimuli presented around the legs. Stettler and Thomas (2017) showed that participants responded significantly faster to visual stimuli that were near (within stepping distance) as opposed to far (outside stepping distance) from the feet, suggesting to the presence of a boundary between PPS and EPS for the feet. Schicke et al. (2009) were one of the first groups to behaviorally show that a PPS representation around the feet exists using a crossmodal congruency task. In this paradigm, the crossmodal congruency effect (CCE) implies that when the visual stimulus is spatially incongruent with the tactile stimulus, tactile reaction times are significantly slowed. The results of Schicke and colleagues revealed that the feet exhibit a CCE of similar magnitude to that of the hands, suggesting that PPS around the feet exists. Further evidence for a lower limb PPS representation comes from the work of Noel and Wallace (2016a). Participants were asked to judge the order of stimulation for vibrations applied to both ankles (while they were crossed or uncrossed) under normal and sensory-deprived (i.e., no vision, no auditory, or no vision and auditory) conditions. They showed that depriving participants of audio and visual information (albeit irrelevant to the task) impaired spatial localization of tactile information on the feet, particularly when the legs were crossed, suggesting that spatial localization of the lower body critically depends on multisensory integration. These findings provide compelling evidence that a peri-foot representation exists, and thus suggest that mapping the size of the peri-foot representation is a feasible aim. Stone et al. (2018) uncovered the boundary between PPS and extrapersonal space (EPS). They found that reaction times to tactile stimuli, for approaching visual stimuli only, showed a systematic decrease related to visual stimulus location. That is, the presence of the approaching visual stimulus boosted tactile processing within 73 cm (but multisensory facilitation remained present in the 67–89 cm range) of the toes.

To summarize, from the studies presented in this paragraph, it is clear that space around us is split in multiple subspaces based on our attentional processes and that these different subspaces use different body schema for a reference.

1.2 Sensory modalities, movement and space representations around the body.

In the previous paragraph, we concentrated our attention on the spaces around the body, without considering the role of sensory modalities. However, we will now review the research on how each sensory modality represents space independently of the others modalities. Our understanding of different roles of each sense on spatial representation come from several different research areas. Neglect is the best pathology to investigate the parcelization of space in multiple parts and to see how different sensory modality can be selectively impaired with regard to understanding the space around the body. Spatial neglect involves an impaired or lost ability to react to or process sensory stimuli — visual, auditory, tactile, even olfactory — present in the hemispace contralateral to the lesion site. Such impairments may occur even when basic primary sensory or motor skills are not impaired Corbetta et al. (2005). Despite the pivotal role of vision in spatial perception, it is possible to distinguish several kinds of neglect based on sensory modality (unisensory modal and mixed), suggesting that spatial representation can be selectively impaired in one sensory modality and remain intact in the other modalities. There are several distinct types of neglect:

Visual neglect that it is the most frequent type of USN. It is defined as the incapacity to detect or respond to stimuli presented in the contralesional visual field (most commomly occurring in the left field of vision) Heilman et al. (2000).

Auditory neglect is defined as inattention to sounds or verbal stimuli stemming from the hemispace contralateral to the lesion Heilman and Valenstein (1972).

Somatosensory neglect, occurs when patients patients ignore tactile, thermal or painful stimuli applied to the contralesional body side. Patients with this type of neglect can also make localization errors or mistakes when evaluating the spatial position of their own limbs Heilman et al. (2000). Somatosensory neglect must be differentiated from primary somatosensory deficits. It can mimic the clinical picture of pseudo-hemianesthesia Heilman et al. (2000). This spatial neglect can also affect proprioception. Vallar et al. (1993, 1995) conducted an experiment in right brain-damaged patients with USN that required participants to evaluate the orientation of their upper limbs, which were set passively into different positions, in the vertical and horizontal planes. These patients presented a perceptual deficit of position sense for their contralesional limb, whether it was positioned in their contralesional or ipsilesional side of space, in the absence of primary sensory deficit to the right hemibody. Spatial neglect patients often also have problems with the processing of body space. At the motor level, such patients may underuse the arm contralateral to the lesion (motor neglect), and make fewer movements toward the neglected side of their body with their healthy arm (hypokinesia).This disorder of space representation may also affect ones ability to estimate the size of visual objects Milner and Harvey (1995) and the position of our body in space Richard et al. (2000). This does not imply that a similar number of neurological processes are involved, but it is possible that the same neural process/or potentially multiple ones is underlye disordered perception, representation and action. This view is consistent with electrophysiological research on spatial performance in neurologically intact monkeys Georgopoulos et al. (1989); Kalaska et al. (1983).

A complex link exists between unilateral spatial neglect (USN) and vision but it does not necessarily co-occur with a visual deficit. Indeed, USN is not a perceptual deficit and it can be observed in non-visual modalities as well as in mental spatial imagery. Neglect symptoms are typically more severe and more persistent in the visual modality than in other sensory modalities Chokron et al. (2002). Chokron et al. (2004) studied the influence of vision on spatial representation in six right brain-damaged patients suffering from left USN. They administered two tasks involving spatial representations: a clock-drawing task and a drawing from memory task in two experimental conditions, with and without visual control. Interesting, they found that in both task, subjects performed better with their eyes closed. This result support the primary role of vision in spatial representation, by showing that the absence of visual feedback may decrease and even suppress left neglect symptoms Bartolomeo et al. (2001); Chokron et al. (2002). Indeed, vision is largely involved in the orientation of attention in space; the suppression of visual control may diminish the attraction towards the right (ipsilesional) hemispace and in doing so allows a re-orientation of attention towards the left neglected hemispace. Summarizing this last part, it is possible to say that our senses can construct different independent spatial maps. The senses may vary in their ability to perceive and process space. Further, each sense may vary in its precision on these tasks. This is true especially during childhood when the brain is plastic and different senses calibrate each other during various tasks. Our perception of the external world relies principally on vision and hearing. Vision is the most reliable sense to perceive the external world. Many species greatly rely on the ability to determine accurately and rapidly the location of a sound source. As general rule, our sensations tend to be dominated by the modality that provides the most detailed and reliable information about the external world. Vision provides highly accurate and detailed spatial information about the three-dimensional properties of external objects. It is used to guide spatial judgements in other modalities as well, and can therefore influence (and sometimes distort) our spatial perception of auditory and tactile events.

Vision

Visual system is probably the most complex of our perceptual systems. It is divided in multiple parts, with different and hierarchical roles. For the present work, it is important to understand the “tools” that this system has for localizing objects in the space. In 1982, Ungerleider and Mishkin (1982) suggested that the understanding of an object’s qualities and of its spatial location depends on the processing of multiple kinds of visual information in the inferior temporal and posterior parietal cortex, respectively. They reported evidence from a number of different types of studies suggesting that these two areas receive independent sets of projections from the striate cortex. They distinguished between a ’ventral stream’ of projections with the end in the inferotemporal cortex, and a ’dorsal stream’ that terminates in the posterior parietal region. The functions of these two pathways were inferred from behavioral studies on animals with lesion. They noted that monkeys with brain injuries in the inferotemporal cortex were profoundly impaired during visual pattern discrimination and recognition tasks Desimone and Gross (1979), but not during solving spatial tasks. Quite the opposite pattern of results was observed in monkeys with posterior parietal lesions Milner et al. (1977); Ungerleider and Mishkin (1982). These observations underpin the model of two visual systems: the inferotemporal circuitry specialized for identifying objects, while the posterior parietal circuitry specialized for spatial perception. According to Livingstone and Hubel (1988) that these two streams can be traced back to the two main cytological subdivisions of retinal ganglion cells: one of these two subdivisions terminates selectively in the parvocellular layer, while the other terminates in the magnocellular layer of the lateral geniculate nucleus (LGN) Livingstone and Hubel (1988); Schiller et al. (1990). Certainly, these ’parvo’ and ’magno’ subdivisions remain relatively segregated at the level of the primary visual cortex (V1) and in the adjacent visual area V2. They also appear to predominate, respectively, the innervation of area V4 and the middle temporal area (MT), which in turn provide the major visual inputs to the inferotemporal and posterior parietal cortex, respectively. However, it is becoming increasingly clear that the separation between magno and parvo information in the cortex is not as distinct as initially thought. In short, it now appears that the dorsal and the ventral streams each receive inputs from both the magno and the parvo pathways. Subsequent studies Milner and Goodale (1992) proposed a new interpretation of the dichotomy between the ventral and dorsal projections. Previous models of how humans make sense of objects assumed people were attending to “what it was” (i.e. visual discrimination of the object) and “where it was” (i.e. spatial discrimination). In contrast, the more current view is that humans are focused on “what it is” and “how to reach it” (i.e. visually guided action). Moreover, vision works in parallel, simultaneously providing a great amount of information from the external word to the brain. This visual dominance stems in part from the brain receiving high-resolution spatial information directly from the retina that is coded topographically throughout the visual pathway. Due to this specialization in spatial perception, vision plays a crucial role in setting up spatial-processing mechanisms during a critical or sensitive period of child development; but after these mechanisms have become functional, children appear to process visual and nonvisual spatial information equally efficiently. In view of vision’s crucial role, it could genuinely be considered to be a spatial modality. This point of view is well explained by the calibration theory, which states that the sense that is more robust and thus more accurate for a specific perceptual task will inform the all other senses during that task; in other words the best sense in terms of precision, reliability and/or consistency will be the calibrating sense and be the most important one for sensory fusion Ernst and Banks (2002); Ghahramani et al. (1997). Vision serves an important role in spatial perception by influencing the maturation of the auditory spatial response properties of neurons in certain regions of the brain. This has been demonstrated most clearly in the superior colliculus (SC) in the midbrain, where visual, auditory and tactile inputs are organized into topographically aligned spatial maps King (2004). This neural organization allows each of the sensory inputs associated with a specific event to be transformed into appropriate motor signals to control gaze direction Hartline et al. (1995); Sparks (1986). The dominant role played by vision in aligning the sensory maps in the SC has been demonstrated by altering the spatial relationship between auditory localization cues and directions in visual space, producing a corresponding shift in the neural representation of auditory space. The advantages of vision over the other sensory modalities appear to be quantitative in nature (more precision, greater amount of available information, etc). These advantages appear to induce a way to encode spatial information that seem qualitatively different from those which are spontaneously implemented in absence of vision (i.e. by blind people).

Hearing

Sound localization is possible due to monaural and binaural cues. Binaural localization of sounds in the horizontal dimension (i.e., judging whether a sound is to our right or our left) involves detecting differences in interaural time and level i.e., interaural time difference/delta

ITD and interlevel difference ILD, respectively). That is, we judge a sound to be in the right hemifield because it reaches the right ear earlier (ITD) and louder (ILD) than the left ear. ITDs is primarily useful for frequencies below 1500 Hz whereas ILDs are best for localize sounds localize sounds with frequencies below and above 1500 Hz Middlebrooks and Green (1991). When one's head and the ears are symmetrical, localization in the vertical median plane (i.e. judging whether a sound in front of us is above or below the eye level) cannot rely on ITDs or ILDs. In this case, localization relies on the direction-dependent changes in the sound spectrum that are generated by the pinna Lopez-Poveda and Meddis (1996). In reverberant environments, we are exposed to both direct sounds as well as the echos that are reflected from the walls of the room. In this situation, the auditory system assigns greater weight to direct sounds than it does to reflected sounds, and localization is based on the cues provided by the direct sound. This phenomenon is known as the 'precedence effect' or echo suppression Wallach et al. (1949). Due to the conformation of the ear, adults are better at localizing sounds in the horizontal (left-right) than in the vertical (above-below) plans and at localizing sounds placed in front than those behind them Middlebrooks and Green (1991). The human brain finds it difficult to disambiguate the position of the sound placed in front of or behind the body. This spatial perceptual ambiguity is known as the cone of confusion Wallach et al. (1949). This is an imaginary cone extending outward from each ear and includes all sound sources produce identical interaural differences. When the binaural information correlates equally well with two opposite spatial locations, reversal errors can occur Carlile et al. (2005); Scharine and Letowski (2005). When these errors occur, the estimation of the sound source's location is perceived to be in the opposite direction to the actual sound location. Front–back (FB) and back–front (BF) errors are the most common reversal errors. However, they are rare for open ear conditions and are most frequent for sound sources located on or near to the median plane Makous and Middlebrooks (1990). Typically, front–back errors are more common than back–front errors, however relative proportion of these errors depends on various factors, including the visibility of the sound sources Chasin and Chong (1999). Monaural cues are more powerful in differentiating between specific positions on the surface of the cone of confusion, as they do not depend on the presence of two ears. They result mostly from sound absorption by the head and the outer ear (pinna) Lopez-Poveda and Meddis (1996); Musicant and Butler (1984). Despite this limitation in spatial localization, Hofman et al. (1998) found that, for spatial representation, the human auditory system is able to adapt to altered spectral cues, which do not interfere with the neural representation of the original cues. This suggests that the hearing system is highly plastic in interpreting new acoustical cues. This last point open new possibilities for training and rehabilitation regarding auditory spatial representation.

Movement

Voluntary actions are able to modify the boundaries between these spaces. Single cell recordings and lesion studies have revealed that the neural systems dedicated to spatial representation and spatial cognition are organsed in a distributed network in which discrete brain areas are devoted to the coding of the different spatial attributes of each stimulus Robertson and Marshall (1993). This network is not based solely on perceptual operations, but it is heavily modulated by the planning of purposeful actions which modify the spatial relation between the subject and the external world. Based on this neurological research, our understanding of space representation has been evolved from considering the “construction of a map of external space” to models of a “locus of integration between perception, action and awareness”. In this current view, the neural processing necessary to grasp an object is closely linked to the neural coding of that object in the external space. Maravita and Iriki (2004); Rizzolatti and Fadiga (1998) showed that voluntary actions have an effect on the activation and modulation of spatial representations especially when there is a change in the spatial extension of the agent’s body, as in tool using which allows someone to reach beyond their normal reaching distance.

To summarize the previous paragraph, we can hypothesize that spatial representation can be impaired in one sensory modality but remain be intact in other senses which suggest that each sensory modality represent space independently of the others. This is possible as that vision and hearing have different “tools” to represent space. Moreover, we have seen that movement has an important role in modulating spatial representation.

1.3 Frame of reference and body representation.

In the previous paragraph, we concentrated on the role of individual sensory modalities in perceiving space. Here we discuss another aspect related to space representation, which is how we build a spatial map. Indeed, space is not something that can be directly experienced through specific sense, as light for vision or frequencies for audition. To build a representation of the space, our brain must to judge a stimulus with respect to a reference. In spatial cognition research, a reference frame defines a mean of representing the locations of entities in space. The two dominant reference frames are the allocentric and the egocentric frames of reference Kosslyn (1987). Egocentric frames of reference use the body or body parts as the center of the environment, whereas allocentric frames of reference are centered on external objects or on the environment itself. Evidence for a neural basis of egocentric and allocentric coordinate reference frames has been reported by Town et al. (2017) , who showed that the early auditory cortex preferentially represents sound source location relative to the body, but that a minority of cells also represent sound location independent of body position. While either egocentric or allocentric frames of reference can theoretically be used to perform most auditory spatial tasks, it is possible that certain tasks can be performed most effectively using an egocentric frame, while others can be performed most effectively using an allocentric frame. Multiple reports in the spatial cognition literature have suggested that, in the absence of vision, individuals primarily rely on egocentric frames of reference to carry out spatial tasks Cattaneo et al. (2008); Coluccia et al. (2009); Latini-Corazzini et al. (2010); Pasqualotto and Proulx (2012). Vision seems to be necessary to develop allocentric frame of reference. Ruggiero et al. (2009) studied persons with different amounts of visual experience: early (congenital) and late (acquired) onset of blindness, short-term deprivation (blindfolded) and full vision (sighted). Their task required either egocentric or allocentric processing of metric relations Iachini et al. (2009); Ruggiero et al. (2009). Subjects had to memorize three-dimensional objects laid on the floor through haptic and locomotor exploration. After a delay, they had to provide spatial judgments of relative distance in relation to either the subject or another object. Results showed that one's visual status altered one's performance on the spatial processing task: participants with congenital blindness showed a specific drop in the allocentric processing as compared to blindfolded and sighted participants, whereas all groups performed similarly in the egocentric processing. Finally, the performance of acquired participants was between that of congenital and sighted groups, suggesting that lack of the visual experience can erode one's ability to process allocentric information Cattaneo et al. (2008). From a theoretical point of view, Millar and Al-Attar (2004) suggest that congenitally blind people are forced to rely on egocentric encoding because the amount of distal information provided by the environment is reduced and the available information is more difficult to be process. Non-visual inputs would be less efficient than visual inputs for determining the relationship between the moving person and the environment. This evidence suggests that vision is particularly efficient in providing information about the allocentric, invariant relationships between objects in external space. Zaehle et al. (2007) studied the neural basis of the egocentric and allocentric spatial frame of reference. They set up an experiment using verbal descriptions of spatial relations either with respect to the listener (egocentric) or without any body-centered references (allocentric) to induce the two different spatial coding strategies. The aim of the study was to identify and distinguish the neuroanatomical correlates of egocentric and allocentric spatial coding without visual stimulation confounds. Results showed that in both conditions, there was involvement of the bilateral fronto-parietal network associated with spatial information processing and activations in primary visual areas in both hemispheres. There was also some neural circuits mediating the different spatial coding strategies. While egocentric spatial coding mainly recruited the precuneus, allocentric coding of space activateed a network comprising the right superior and inferior parietal lobe and the ventrolateral occipito-temporal cortex bilaterally. Furthermore, bilateral hippocampal involvement was observed during allocentric, but not during egocentric spatial processing. These fMRI results demonstrate that the processing of egocentric spatial relations is mediated by medial superior–posterior areas, whereas allocentric spatial coding requires an additional involvement of right parietal cortex, the ventral visual stream and the hippocampal formation. These data suggest the existence of a hierarchically organized processing system, in which the egocentric spatial coding requires only a subsystem of the processing resources of the allocentric condition.

To summarize, it was shown that our brain conceptualizes space/s using primarily 2 strategies: egocentric referencing by constructing a spatial representation with respect to the body (or part of the body) and an allocentric referencing strategy based on representing an object with respect to another object. Different studies have shown that senses are differently able to build a representation of space trough these two strategies. Vision appears to play a crucial role in developing allocentric reference of frame. This is particularly true during childhood, when vision calibrates hearing in spatial tasks.

1.4 Sensory cortex as task specific operators

While in the previous paragraph we focused on how from sensory input, our brain builds a spatial map, in this paragraph we will present a different (not contrasting) point of view regarding how the concept of space is further informed by visual input, independently from the sensory input received. In traditional neuroscience, functional brain specializations were considered to arise during evolution through natural selection and to be constrained to specific sensory modalities. These assumptions were supported by anatomical consistencies of brain specializations across individuals for the broad sensory division of labor (e.g. visual or auditory regions). In the blind population, it has been shown that the ‘visual’ cortex has been plastically recruited to process other modalities, and even language and memory tasks (reviewed in Frasnelli et al. (2011); Merabet and Pascual-Leone (2010)). Many of these changes start to occur within days following the onset of blindness, and therefore affect not only the congenitally blind but also, though probably to a different extent, in those who lose their vision early or later in life. Brain areas are highly flexible sensory-independent task-specific operators, and given adequate training can change the type of sensory input they use to retrieve task-relevant information within a matter of hours to weeks. A growing body of evidence, however, has accumulated in the past decade that casts doubts on the canonical view of the sensory-specific brain. This evidence demonstrates that, in both sighted and blind individuals, the occipital visual cortex is not purely visual and that its functional specialization is independent of visual input, leading to the hypothesis that the brain may actually be task-oriented and sensory modality independent Reich et al. (2011); Vannuscorps et al. (2018). Furthermore, recent evidence has shown that in some cases the same specialization emerges even without any visual experience or memories (as assessed by studying people who are born completely blind; Amedi et al. (2007); Collignon et al. (2011); Fiehler et al. (2009); Mahon et al. (2009); Matteau et al. (2010); Reich et al. (2011)), and that this specialization emerges rapidly once the brain is trained to interpret the relevant information, suggesting that the cortical functional specialization can be attributed at least partially to innately determined constraints Vannuscorps et al. (2018). This task selectivity was demonstrated for a variety of tasks and brain areas, including selectivity to nonvisual motion in the visual middle temporal area Matteau et al. (2010), to tactile object recognition in the lateral-occipital complex (LOC) Amedi et al. (2001, 2010); Tal and Amedi (2009); and to sound localization in the middle-occipital gyrus (MOG) Collignon et al. (2006).

To summarize, these studies together suggest that sensory cortex do not simply elaborate specific sensory information (as light, in visual cortex), but they are the operators/machines for higher cognitive skills that are independent by sensory modalities (i.e. visual cortex in spatial representation).

1.5 Goal of the study

In this work, I investigated if the pivotal role of vision in representing space can produce differentiation between portions of space.

To date, several studies have investigated the audio perception across spaces, for example, Farnè and Làdavas (2002b); Zampini et al. (2007) studied the front and back space, Heed and Röder (2010); Scandola et al. (2016) studied the high and low space separately, while Viaud-Delmon et al. (2014); Weiss et al. (2011) studied the effect of actions on audio perception. However, no one has yet experimentally compared the spatial representation of these areas. It is important to understand how we represent the space around us, as spatial representation skill is at the base of a good interaction with the environment. To see if the different availibility of sensory modalities across spaces produces a different ability to represent these spaces, we tested auditory spatial representation of sighted individuals in space where the visual information is naturally availabe (e.g. front space) and where it is not (e.g. back space). Moreover, we administred the same tasks to a group of blind individuals, for which the same difference should not be evident.Finally, we tested audio-motor integration could improve spatial representation in space where vision is not present. In this way we could appreciate the role of vision in calibrating hearing in different spaces.

Chapter 2

Spaces around the body

Studies on neglect patients have shown that the space around our body is not represented by the brain as a unitary dimension. These Farnè and Làdavas (2002a); Saj and Vuilleumier (2007); Vallar et al. (1995); Viaud-Delmon et al. (2007) showed that the brain split the space in several portions on the base of attentional mechanisms. However, it is still unknown if the different sensory input available around the body space, contribute to split the space in multiple subspaces differently coded by the brain. It is known that vision is important in developing spatial cognition. However, not every spaces around the body are visual spaces (i.e.the back space) and it is unknown how this lackness affects spatial representation.

On one hand, the sensory compensation hypothesis Braun (2016) states that the lack of a sensory ability (e.g. vision), leads to an improved ability of non-visual senses. Studies on blind subjects support the idea that this enhanced auditory ability is due to cross-modal plasticity Collignon et al. (2009); Voss et al. (2011). The visual cortex is highly plastic; this is more evident in young animals, but it is still present in adulthood. This plasticity allows the visual cortex in congenitally blind people to become colonized by other sensory systems (i.e. auditory and somatosensory) Sadato et al. (1996); Weeks et al. (2000). Few days of binocular deprivation is sufficient for the primary visual cortex to be colonized by touch Merabet et al. (2008). There is psychophysical evidence that the congenitally blind have enhanced tactile discrimination Goldreich and Kanics (2003), auditory pitch discrimination Voss et al. (2004a), sound localization Lessard et al. (1998); Teder-Sälejärvi et al. (1999), and are able to properly form spatial topographical maps Fortin et al. (2008); Tinti et al. (2006). Spatial hearing tasks have been shown to activate the visual cortex of early blind individuals Dormal and Collignon (2011); Fortin et al. (2008); Gougoux et al. (2005); Weeks et al. (2000) and individual localization abilities have been shown to correlate with the magnitude of visual cortical activity Fortin et al. (2008); Gougoux et al. (2005); Voss et al. (2008, 2011). Interestingly, the enhancement is not uniform, but depends somewhat on the space considered. For example, localization of peripheral, but not central stimuli exceeds that of controls Teder-Sälejärvi et al. (1999), and is similar for the localization along the horizontal, but poorer for the vertical meridian. This is consistent with anatomical evidence showing that the peripheral visual field has strong auditory projectionsFalchier et al. (2002), possibly facilitating colonization. On the other hand, the general-loss hypothesis states that vision has a pivotal role in developing spatial cognition Bremmer et al. (2002); Pasqualotto and Proulx (2012); Warren (1974). Indeed, vision allows multiple stimuli to be judged simultaneously, leading to the possibility of building spatial relationships between objects displaced around us Noel and Wallace (2016b). This key role of vision in spatial perception is explained well by the sensory calibration theory, which states that the more accurate sense teaches (calibrates) the others; when one calibrating modality is missing, the other modalities result impaired. Children with visual disabilities have problems in understanding the haptic or auditory perception of space Cappagli et al. (2015) and children with motor disabilities have problems in understanding the visual dimension of objectsGori et al. (2011). This theory shows that congenitally blind people are impaired in several spatial tasks Cappagli et al. (2015); Finocchietti et al. (2015); Gori (2015); Gori et al. (2014); Kolarik et al. (2013); Lewald (2002); Vercillo et al. (2016). The auditory spatial impairment in some tasks, such as in spatial bisection, seems to be related to the inability to build a spatial metric between soundsGori et al. (2014). Spatial bisection task is adopted to investigate spatial metric, which requires using allocentric reference frame. In the spatial bisection task, three successive sounds are presented from three different spatial locations and the participant is required to report whether the second sound was closer to the first or the third Merabet and Pascual-Leone (2010); Sadato et al. (1996). It has usually been assumed that spatial bisection is performed most efficiently using an allocentric reference frame, as this allows direct assessment of the positions of different sound sources (as opposed to referring the position of each source to the head/body and then inferring the spatial separation of the sources). Minimum audible angle task is another common task used to evaluate spatial acuity. It does not required the building of spatial representation. In a minimum audible angle (MAA) task, two successive sounds are presented at different spatial locations and the participant is required to report whether the second sound is to the right or the left of the first sound Sadato et al. (1996); Viaud-Delmon et al. (2007). It has been assumed that the MAA task “requires a spatial judgment that might be more anchored to an egocentric reference frame rather than an external reference frame” Sadato et al. (1996), although in principle the MAA task could be performed using either an egocentric or an allocentric frame of reference.

It has been reported that blind participants show poorer performance on a bisection task than sighted participants, whereas sighted and blind participants show similar performance for an MAA task Sadato et al. (1996); Weeks et al. (2000) and for an auditory localizatioell represented because of the lack of vision.ry for the development of spatial cognition, the back space could be not wn task involving comparisons of a sound source to with the position of the participant's own hand, which is assumed to be based on the use of an egocentric frame of reference Merabet and Pascual-Leone (2010). These findings have been interpreted as indicating that blindness is associated with a lack of ability to use an allocentric reference frame, such that blind participants rely on an egocentric frame of reference to perform all spatial tasks. Mapping of the positions of auditory signals into external co-ordinates occurs during the individual's development as a result of visual inputVoss et al. (2004a), and the poorer performance of blind participants for the bisection task has been suggested to support the idea that the bisection task requires or is more anchored to an allocentric frame of reference Merabet and Pascual-Leone (2010). On the base of these evidences, we hypothesize that If vision is important in spatial representation and its influence is spatial related, then we might expect visual and non-visual spaces to be differently represented. In the following studies, we adopted bisection and MAA tasks to assess the role of vision and the frame of reference adopted in different portions of space.

2.1 Exp 1: Role of senses in representing spaces around the body

As we have seen, visual modality is crucial to develop audio spatial metric (as found in bisection task Gori et al. (2014)). Indeed, as shown by Gori et al. (2014), blind people are not able to solve this task, while they perform like sighted people the minimum audible angle (MAA) and temporal bisection task.

Since also in sighted people, the visual information is not available in the back space, it is possible that front and back auditory space are differently developed. In particular in this experiment, we hypothesized that vision is necessary to develop spatial cognition. If so, it is possible that the back space is under represented, because of the important role of vision is naturally absent. To test this hypothesis, we asked to sighted subjects to perform the spatial bisection task in front and back space.

2.1.1 Method

Twenty-three subjects (7 females and 16males) aged 28 ± 11years (mean± SD) were tested in spatial bisection task, minimum audible angle and the temporal bisection task, in a randomized order (Figure 2.1). In order to have no notion of the room or the speaker layout, subjects were blindfolded before entering an experimental room (echoic). Subjects were standing at a distance of 80 cm from the stimuli and aligned with the center of a bank of 11 speakers, spanning respectively ± 23.6° of visual angle, at ear level and ± 9.9° at foot level, the distance between two near speakers was of 7 cm. We used an onset abrupt pink noise lasting 100 ms, for which both interaural time differences and interaural level differences are important; the sound was well heard from every subjects. For the spatial bisection task, three 100 ms stimuli were presented successively at 500 ms intervals between 11 speakers, the first at -23.6°(at ear level) or -9.9° (at foot level), the third at +23.6°(at ear level) or +9.9°(at foot level), based on condition, and the second at an intermediate speaker (between the first and third sound, 9 possible speakers) position determined by the QUEST adaptive algorithm, which estimates the point of subjective equality after each response, and places the next trial near that estimate. Subjects reported verbally whether the second sound was closer to the first or to the last sound. Each subject performed 60 trials for each condition. For the minimal audible angle task, two 100 ms stimuli of 500 Hz were presented successively with a 500 ms interval, one (randomly first or second) on the central speaker (0°), the other at a certain distance left or right, following the QUEST algorithm. Each task was carried out at two elevations (ear and foot level) and in two different positions (front and back), resulting in four randomized conditions: frontal ear, frontal foot, back ear and back foot space (Fig. 1). In order to perform the task in allocentric coordinates, the spatial order of the three sounds was always the same, independent from the position of the subjects. This means that, in the frontal condition of the bisection task, the first sounds started from the left of the subjects' position, while in the back condition the sound started from the right (same absolute position in the space but different in relation to the body). In the MAA, in the frontal conditions the subjects reported which of the two sounds was located further right, and in the back conditions, which was further left (see Fig. 1). Each subject performed 60 trials for each condition. For the spatial bisection task, the proportion of "third" responses was calculated for each speaker distance, while for the MAA task the proportion of right or left (in accordance with condition) was calculated. The temporal bisection task was used as a control task in order to ensure that sounds coming from the four quadrants were similarly perceived. The task is similar to the spatial bisection, except that all sounds were played on the central speaker (0°), and subjects reported verbally whether the middle sound was temporally closer to the first or the last (the total duration was still 1 s, but the second stimulus varied in time, following the QUEST algorithm). For all tasks, results were fitted by Gaussian error functions whose standard deviation estimated threshold. Most subjects completed all the tasks in one session, with an interval between each task and each condition. 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) and conducted in line with the Declaration of Helsinki.

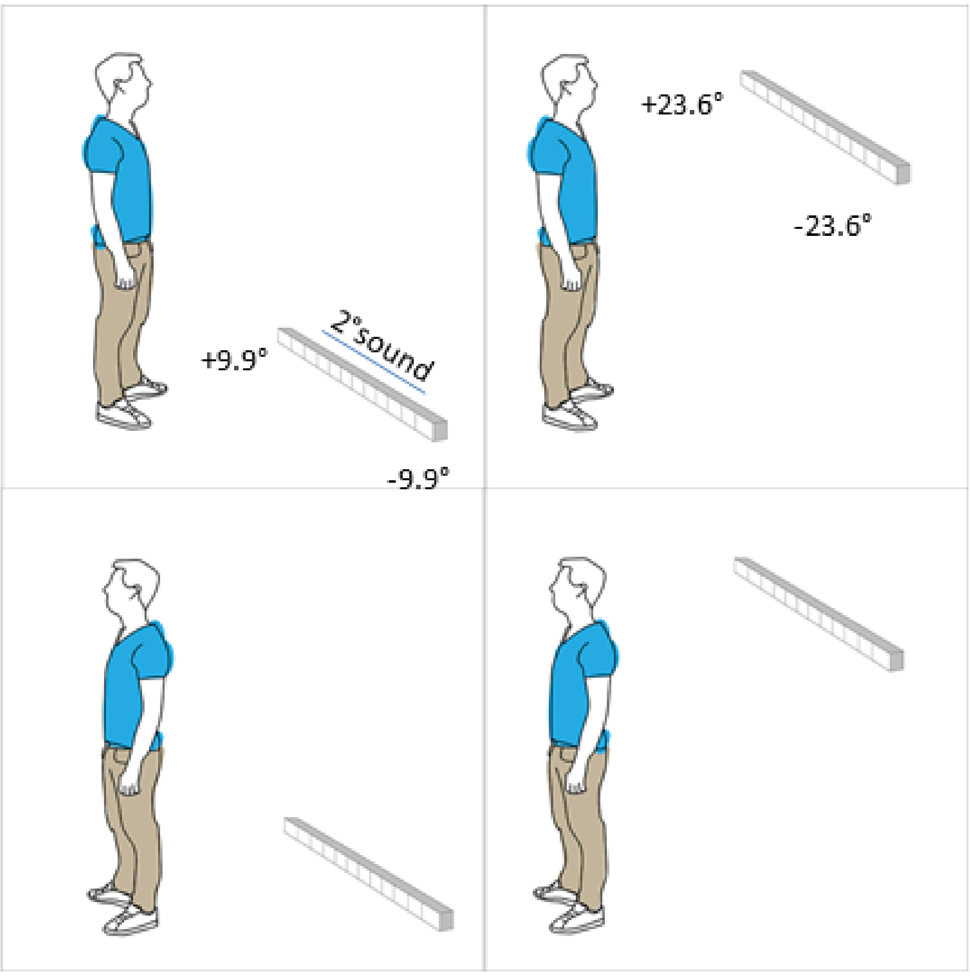

Figure 2.1 The spatial bisection task was performed at ear and foot level in both frontal and rear space. Three sounds were delivered from the three different speakers. Subjects had to judge whether the second sound was closer to the first or to the last sound. The spatial order of the three sounds was fixed in the space (they always started from the same speaker). Minimum audible angle task: the task was performed at ear and foot level in both frontal and rear space. Subjects had to judge the position of two sounds. In the frontal condition, subjects had to report which of the two sounds was further right, while in the rear condition, they had to state which of the two sounds was further left. Temporal bisection was performed at ear and foot level in both frontal and rear space. Three sounds were delivered from the same speaker with different delays between each other, and subjects had to judge which was the shortest interval between sounds.

2.1.2 Results

For each condition, a psychometric function was calculated.
For each subject and condition, the space constant (σ) of the fit was taken as the estimate of threshold for all tasks. Space constants were converted from centimeters to angles. However, the distance of speakers from the ears was different at ear level (80 cm) and foot level (200 cm), thus corresponding to different visual angles between the first and third sound ($\pm 23.6°$respectively). Therefore, in a first analysis, we considered each level separately and we compared front and back position with a paired two tailed t-test and we considered $P < 0.05$ as significant, after applying Bonferroni correction for multiple comparisons (mean and standard error are reported). A T test performed on the spatial bisection (Figure 2.2left)at earlevel showed a significantlylower(threshold),($t_{(22)}$ =-4.7,$P < 0.01$)in the frontal space(4.1 ± 0.6)compared to the back space (6.8+/-0.7). The same analysis performed on the MAA($t_{(22)}$=-1.9,P=0.06), (Figure 2.2center) and on thetemporal bisection tasks ($t_{(22)}$=-0.3, P = 0.7), (Figure 2.2right) showed no difference between frontal and rear space. This result is clearly shown in.(Figure 2.2), where results from the three tasks are reported. Blue bars represent the threshold obtained for the back space, while the red bar represents the frontal space. As can be seen, no differences are reported between threshold for the front and rear space in the MAA, while a significant lower precision (higher threshold) is evident in the back space during the spatial bisection task

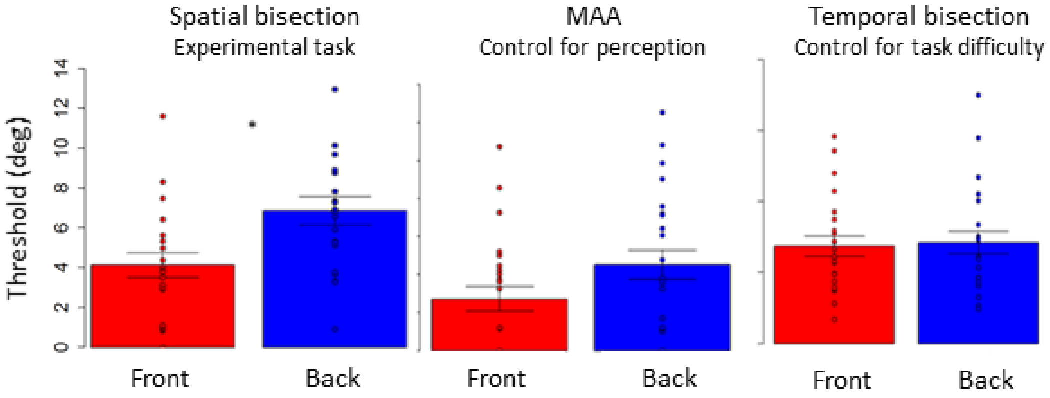

Figure 2.2 red bar reports threshold (deg) for frontal condition, while blue bar refers to back condition. Dots represent the performance of each subject. Error bars represent standard errors. As can be seen, subjects were more precise in the frontal space than in the back, suggesting that vision plays an important role in calibrating spatial hearing. No difference between frontal and back was found in the MAA and temporal bisection.∗ Indicated $p<0.05$

To be sure that the higher precision (lower threshold) in the frontal space was not an effect of higher saliency of space around the face, the same comparison was performed for the threshold obtained for the test carried out at foot level. Exactly the same pattern of results was found at foot level. As reported in (Figure 2.3), higher precision (lower threshold) is present when performing the spatial bisection task in the frontal space than in the back space ($t_{(22)}$ =-2.2,P<0.01), while no difference was observed between front and back in the MAA ($t_{(22)}$ =-0.3,P=0.7) and temporal bisection ($t_{(22)}$ =-0.007,P=1).

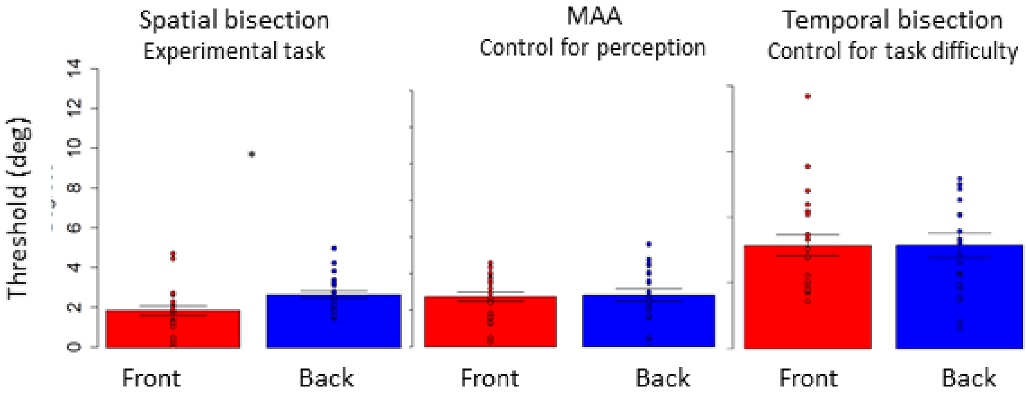

Figure 2.3 Red bar reports threshold (deg) for frontal condition, while blue bar refers to back condition. Dots represent the performance of each subject. Error bars represent standard errors. As can be seen, subjects were more precise in the frontal space than in the back. No difference between frontal and back was found in the MAA.$*$ Indicated p<0.05

To find out whether the difference in precision (threshold) at ear and foot level was similar, in a second analysis, we normalized the data by comparing the different degrees sustained by the device at ear and at foot level. Specifically, each angle was divided by the angle corresponding to the span between the first and the last speaker of the relative elevation (i.e. angles at foot level were divided by 19.8°, while angles at ear level by 47.3°). Results are reported in (Figure 2.4) We performed three independent repeated measure anovas considering sound level (ear vs. foot level) and sound position (front vs. back). Significant results were analyzed by a paired two tailed t-test and we considered $P < 0.05$ as significant, after applying Bonferroni correction for multiple comparisons. Anova on the spatial bisection showed a significant effect of sound position ($F_{(1,22)} = 34$, $P < 0.01$, generalized eta squared (ges) = 0.15). As can be seen in the top of (Figure 2.4),higher precision (lower threshold) (t_{22} =-5,$P<0.01$) was found in the frontal(red bar)space(0.09±0.01),compared to the back(blue) space (0.14±0.01). While no differences were found between sound level ($F_{(1,22)}$ =0.38, P = 0.5, ges = 0.005), as shown in the bottom left of (Figure 2.4), where performance at ear (yellow) and foot (green) level were practically the same, excluding sound distortion due to the floor. Interestingly, the opposite pattern emerged in the MAA, where similar levels of accuracy were reported between frontal and rear space (P = 0.1). On the other hand, different precision (threshold) was found between ear and foot level ($F_{(1,22)} = 21$, $P < 0.01$, ges = 0.16). This result is clearly shown at the bottom right of (Figure 2.4) as can be seen, precision (threshold) at ear (yellow bar) and foot (green bar) level is significantly different ($t_{(22)}$ =-4,$P<0.01$), showing higher precision (lower threshold) for the task performed at ear level (0.07±0.01) compared with foot level (0.13 ±0.01).

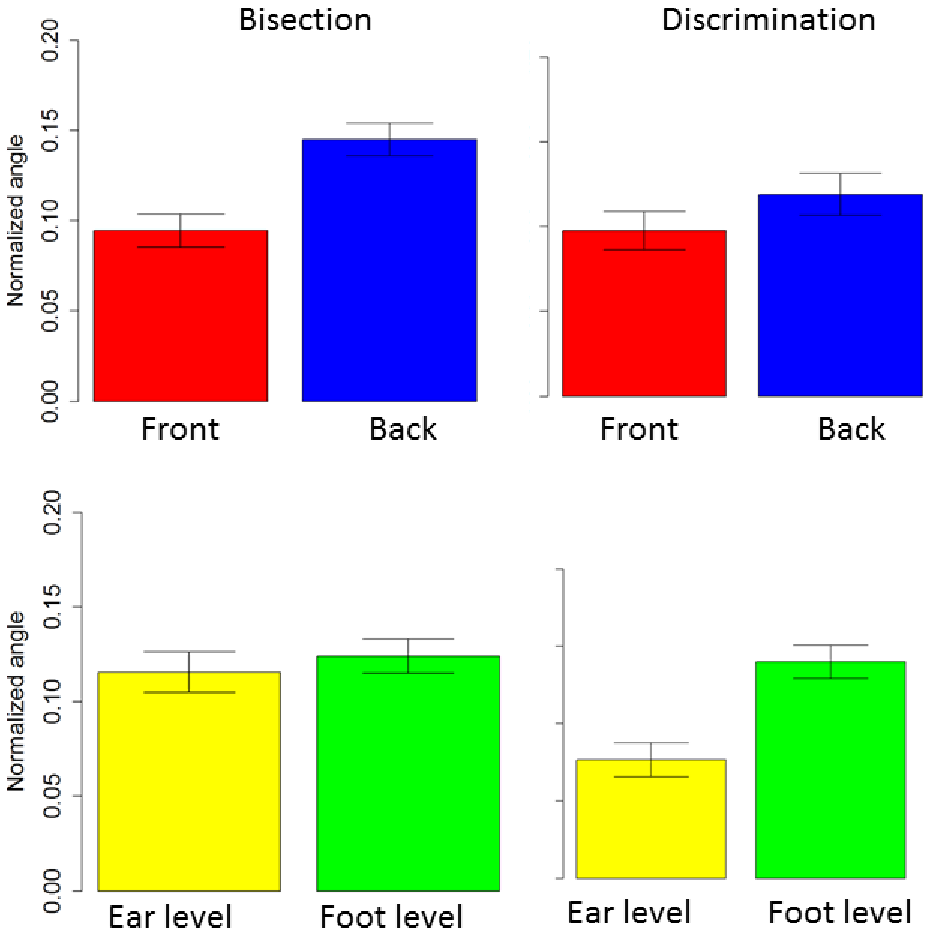

Figure 2.4 red bar reports threshold (deg) for frontal condition, while blue bar refers to back condition. Dots represent the performance of each subject. Error bars represent standard errors. As can be seen, in the bisection task, subjects were more precise in the frontal space than in the back, suggesting that vision plays an important role in calibrating spatial hearing, while no difference were found between ear (yellow) and foot (green) level. An opposite pattern was found in the MAA: no difference between frontal and back, while a difference was found between ear and foot level. ∗Indicated $P<0.05$.

Significantly, no differences between factors were found in the temporal bisection threshold ($P > 0.05$), as reported in (Figure 2.5), suggesting that the complexity of performing the bisection task was similar for the 4 spaces. These results strongly suggest that the auditory metric of sounds coming from the front and back space is differently mapped in space, and that MAA and spatial bisection tasks rely on different cognitive mechanisms.

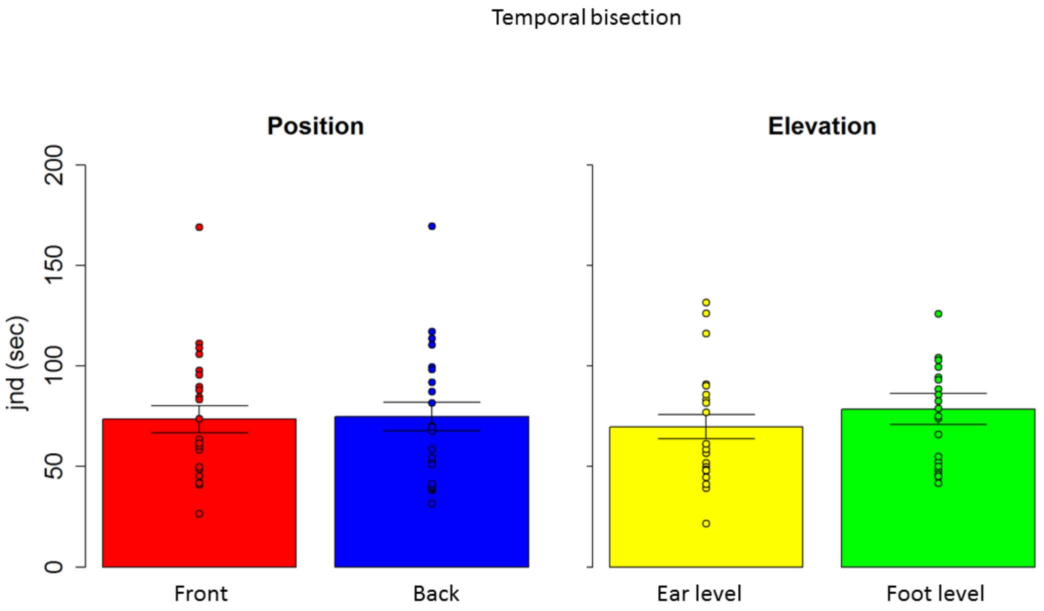

Figure 2.5 red bar reports threshold (sec) for frontal condition, while blue bar refers to back condition. Yellow bar refers to ear level, while green bar refers to foot level. Dots represent the performance of each subject. Error bars represent standard errors. As can be seen, no difference between front and back conditions was found at either ear or foot level. Dots represent the performance of each subject

2.1.3 Conclusions of the experiment

This experiment was designed to test the influence of vision on spatial cognition. Different spaces, in which vision is differently available, were compared. It was already well proved that vision is necessary to develop spatial cognition, but it was still unknown if cognitive spatial skills were spatial or not spatial confined. Results showed that subjects are differently able to represent complex auditory scene (as required by spatial bisection task) in the frontal and back spaces. Importantly, the difference between spaces was evident only in the bisection task and not for the minimum audible angle or for the temporal bisection task.This suggest that front and back spaces differ in terms of degree of spatial representation (as emerged by spatial bisection task) but not for spatial acuity (tested by MAA) and cognitive demand (tested by temporal bisection task). The influence of vision was present at both body levels considered: at the ear and at the foot level, suggesting that visual calibtation extends to every spaces reachable by vision.

Interesting, indipendently by front/back spaces, we found that the MAA was better performed at ears than foot level, while the opposite was true for the bisection task. This result suggest that ear and foot space differ in terms of the frame of references used to represent these 2 spaces. This results suggest that at hear level we can easly use ego and allocentric frame of reference, while at foot level, we perform better when using an allocentric frame of reference. This difference could be due to the saliency of the head that permits to localize a point in the space on the base of head position. The same process could be harder at foot level

2.2 Exp2: Space lateral to the body: the use of an allocentric or egocentric frame of reference

While visual information is differently available in the front and the back spaces, leading to a sharp difference in spatial representatio, in the peripheral space (i.e. longitudinal space lateral to the body) hearing is subjected to cone of confusion and vision is less accurated. Studies on blind Voss et al. (2015) and on deaf people Bottari et al. (2010) showed as, when one sense is lacking, the other senses enanche their performance in detecting stimuli coming from the peripheral space. However, it is still unkown if this sensory plasticity and the presence of cone of confusion make this space different from the frontal and back spaces. So, in the second experiment we investigated the spatial representation and the internal representations (allocentric vs egocentric) of front, back and lateral spaces.
To this end, spatial bisection and minimum audible angle were assessed in frontal, rear and latera spaces. Localization resolution, as measured by the MAA, is greatest for sounds that are straight ahead or behind (as seen in exp 1), but is poorer in lateral space Middlebrooks and Green (1991). Indeed, many positions of sound sources in lateral space lead to almost the same ITD and ILD, producing the so-called "cone of confusion" and leading to problems in distinguishing front from back sounds that may affect performance for an MAA task. The goals of this experiment are two.

First to investigate if different portion of space are represented by different frame of reference. To do this, performance for azimuthal auditory spatial bisection and MAA tasks, was measured in sighted individuals, in three regions of space (front, back, and lateral relative to the participant). This allowed us to assess whether internal representations differed with spatial region. In spaces represented allocentrically the bisection task should be performed better, while in spaces represented egocentrically the MAA task should be performed better.

Second to investigate spatial representation of the lateral space. Indeed, in this spatial region localization resolution, as measured by the MAA, is poorer Middlebrooks and Green (1991); Voss et al. (2004b). Many positions of sound sources in lateral space lead to almost the same interaural time difference (ITD) and interaural level difference (ILD), giving the so-called "cone of confusion" and leading to problems in distinguishing front from back sounds. For these reason, we were interested to investigated if our brain uses a specific strategy (and which) to localize sound in this portion of space.

In summary, in this study we compared spatial bisection and MAA performance for the three spatial regions. As MAA performance has been reported to be higher for sounds in front or back space and is poorer in lateral space, we hypothesized that MAA performance would be worse than bisection performance for sounds presented in lateral space due to front-back ambiguity affecting MAA but not bisection performance, while the opposite was expected for stimuli presented frontally or from the back of the participant, consistent with previous findings for frontally presented sounds only.

2.2.1 Method

Eighteen normally-sighted participants (mean age: 38.5 years, SD = 8.4 years, 9 female and 9 male) were tested. All participants confirmed that they had no cognitive impairments. Audiometric thresholds were measured using the procedure recommended by the British Society of Audiology. All participants had normal or near-normal hearing, defined as pure-tone average (PTA) better-ear hearing thresholds across 0.5, 1, 2, 4 and 8 kHz 25 dB HL. All participants gave written informed consent before starting the test. The study was approved by the Anglia Ruskin Research Ethics Panel and conducted in line with the Declaration of Helsinki. Subjects were blindfolded before entering a quiet room, to prevent them having any knowledge of the room or the loudspeaker layout prior to or during testing. The room contained painted walls, with a tiled ceiling and carpeted floor. The position of the participant during each task was continuously monitored by the experimenter to ensure that they stayed still. Participants were instructed that they would hear sounds originating from loudspeakers positioned around them. Sounds were presented via an array of 11 loudspeakers, which were positioned in an arc on a table at a height of 1 m (Figure 2.6). The centers of the loudspeakers were separated by 10 cm. The loudspeaker array was in the approximate center of the room. The participant was seated 1.3 m from the loudspeakers, and was positioned so that the sounds were presented at 0° elevation. Participants performed spatial bisection and MAA tasks ((Figure 2.6) panels a and b, respectively), as described below. Each task was carried out for three spatial regions relative to the participant: frontally (with the midpoint of the loudspeaker array at 0° azimuth), laterally (midpoint of the loudspeaker array at +90° azimuth for half of the participants, selected randomly, and 90° for the other half), or from the back (midpoint of the loudspeaker array at 180° azimuth). Stimuli were white noise bursts with a frequency range from 20 to 20000 Hz, with a duration of 100 ms and 10 ms rise/fall times, sampled at 44.1 kHz with 16-bit resolution. The inter-stimulus interval was 500 ms. Sounds were generated on an Asus AA185 computer with Realtek High Definition sound card and routed to the appropriate loudspeaker using a MATLAB (Mathworks, Natick, MA) script. Responses were recorded using a MATLAB script. Stimuli were presented at a mean level of 65 dB SPL (unweighted). Bisection task: For the bisection task, participants heard three sounds in each trial. The first and third sounds, referred to as reference sounds, were spatially jittered. The first (reference) sound was presented randomly from the loudspeaker positioned at ±26.5°, ±22.75°, or ±19°, and the third (reference) sound was presented on the other side of the array at ±19°, ±22.75°, or ±26.5°, such that the two reference sounds were always separated by 45.5°. The second sound, referred to as the probe, was presented from an intermediate loudspeaker (between those for the first and third sounds, from 7 possible loudspeakers). Participants reported verbally whether the second stimulus was closer to the right or left sound, and their response was recorded by the experimenter using the response interface. Jittering the spatial locations of the references from trial to trial prevented participants from attending only to the lateral position of the probe relative to the midline and ignoring the reference sounds. The position of the probe for each trial was determined by the QUEST adaptive algorithm, which estimated the point of subjective equality (PSE, the probe position that was perceived to be equally distant from the two reference loudspeakers) after each response, and placed the probe for the next trial near that estimate. The position of the probe within QUEST was coded relative to the positions of the two reference sounds. Three QUEST runs of 20 trials each were interleaved randomly. There were 60 trials for each spatial region. Data collection lasted approximately 1 hour. MAA task: For the MAA task, participants heard two sounds in each trial. The reference sound was presented randomly first or second from the central loudspeaker in the array, and the probe sound presented from one of the other loudspeakers. For the front/back spatial regions, the task was to report whether the first or second sound was perceived to be more to the right. For the lateral region, the task was to report which sound was perceived to be located farthest forward. Responses were recorded by the experimenter using the response interface. The position of the probe was provided by the QUEST procedure on the basis of the previous responses of the subject. The task took 30 minutes in total. The spatial bisection and the MAA tasks were performed in a randomized order. For each task, performance in each spatial region (front, back, or lateral) was assessed. The order of presentation of tasks and spatial region was randomized between subjects. For both tasks no feedback was given and response time was not constrained.

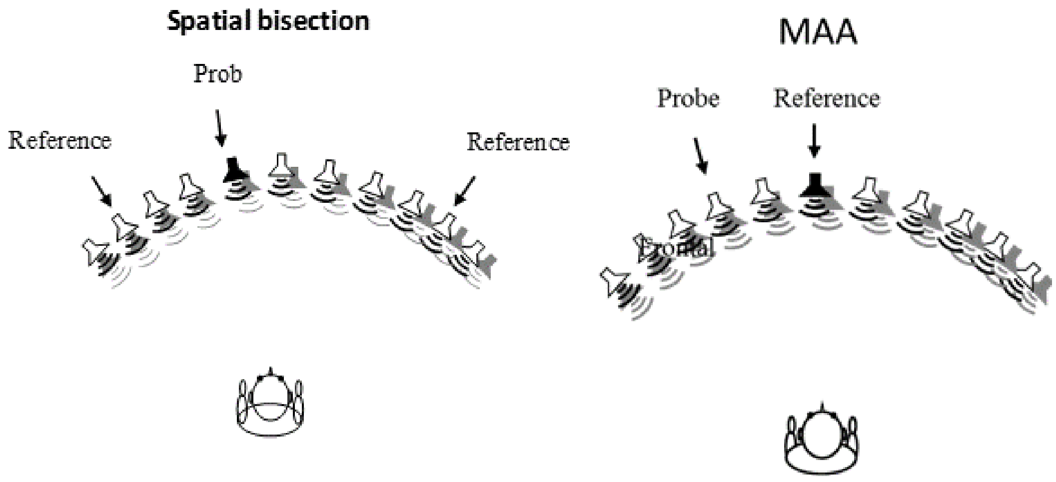

Figure 2.6 ,with examples of possible reference and probe sounds. For both tasks, the participant was oriented so that sounds were presented from in front, laterally, or from the back.

2.2.2 Results

For the spatial bisection task, the probability of the response that the second sound was closer to the rightwards reference sound was calculated for each relative loudspeaker position, while for the MAA task the proportion of responses 'closer to the right position/farthest forward' was computed for each location of the probe stimulus. Both sets of data were fitted by cumulative Gaussian functions. For each participant and condition, the standard deviation (*sigma*) of the fit, which provides an estimate of the slope of the psychometric function, was taken as the estimate of threshold/precision, and the midpoint of the function was taken as the Point of Subjective Equality (PSE). (Figure 2.7) shows mean thresholds and PSEs for MAA and bisection tasks in the upper and lower panels respectively, for front, back and lateral spatial regions. A repeated-measures analysis of variance (ANOVA) was performed on the mean thresholds for the three reference positions with factors spatial region (front, back and lateral) and task (bisection and MAA). Post hoc comparisons were conducted using paired t-tests, and $p<0.05$ was considered as significant, after applying Bonferroni correction for multiple comparisons. There was a main effect of spatial region ($F_{(2,34)} = 23.0$, $p<0.01$, generalized eta squared (ges) = 0.33). No differences were found between front and back spaces ($t_{(17)} = 1.9$, $p = 0.02$), but performance was better for front than for the lateral space ($t_{(17)} = 4.6$, $p<0.01$) and for back than for lateral space ($t_{(17)} =4.3$, $p<0.01$). A significant interaction was found between spatial region and task ($F_{(2,34)} = 10.0$, $p<0.01$, ges = 0.16).

For front space (Figure 2.7 left upper panel) the threshold was lower for the MAA task (red bar) than for the bisection task (yellow bar) ($t_{(17)} = 2.4$, $p = 0.02$). The same pattern occurred for back space (Figure 2.7center upper panel); the threshold was lower for the MAA task than for the bisection task ($t_{(17)} = 2.3$, $p = 0.03$). The opposite pattern was observed for lateral space (Figure 2.7 right upper panel), for which threshold was higher for the MAA task than for the bisection task ($t_{(17)} = 2.8$, $p = 0.01$). An analysis of the effect of spatial region on performance in the bisection task showed that the mean threshold was higher for lateral space than for front space ($t_{(17)} = 2.5$, $p = 0.03$) and for back space ($t_{(17)} = 2.3$, $p = 0.05$). There was no significant difference between mean thresholds for front and back space ($t_{(17)} = 1.5$, $p = 0.2$). Analysis of the bias (the distance of the PSE from the physical center point) showed no significant differences between tasks ($F_{(1,17)} = 2.6$, $p > 0.05$, ges = 0.01) or spatial regions($F_{(2,34)} = 0.6$, $p > 0.05$, ges = 0.16), but a significant interaction ($F_{(2,34)} = 3.2$, $p = 0.048$, ges = 0.4). As can be seen in(Figure 2.7 lower panels), in front space, bias was smaller for the bisection task than for the discrimination task ($t_{(17)} = 6.6$, $p < 0.01$), and the same was true for back space ($t_{(17)} = 3.2$, $p < 0.01$), but no difference was found for lateral space $t_{(17)} = 0.6$, $p > 0.05$).

The right panel of (Figure 2.8)shows the effect of spatial region on performance in the bisection task. The mean threshold was lower for front space (red bar) than for back space (blue bar) ($t_{(17)} = 3.9$, $p < 0.01$) and lateral space (green bar) ($t_{(17)}$ 5.4, $p < 0.01$), consistent with the idea that auditory calibration by vision is more efficient in the central part of front space. There was no significant difference between thresholds for lateral and back space ($t_{(17)} = 1.6$, $p = 0.4$). The MAA thresholds were higher than bisection thresholds with the midpoint at 0o for lateral space ($t_{(17)} = 3.1$, $p < 0.01$), replicating the result obtained in the analysis where data were averaged across reference positions. As previously reported 9, no difference in performance was observed between front and back space for the MAA task ($t_{(17)} = 1.1$, $p = 0.8$, (Figure 2.8 left panel), while thresholds were higher for lateral space than for both front ($t_{(17)} = 4.8$, $p < 0.01$) and back ($t_{(17)} = 4.4$, $p < 0.01$) spaces. For front space, thresholds were low for both tasks, while in back space, performance was better for the MAA task than for the bisection task ($t_{(17)} = 2.2$, $p = 0.04$). The same analysis on PSE values showed no main effect of space ($F_{(2,34)} = 0.4$, $p = 0.6$, ges = 0.01), no effect of task ($F_{(2,17)} = 2.9$, $p = 0.1$, ges = 0.02), and no interaction between task and space ($F_{(2,34)} = 2.3$, $p = 0.1$, ges = 0.03).

Previous work on spatial bisection utilized a fixed midpoint at 0°, rather than a randomized midpoint as was used in the current study. In order to compare the current results with the literature, we estimated bisection thresholds obtained using the fixed midpoint at 0° and

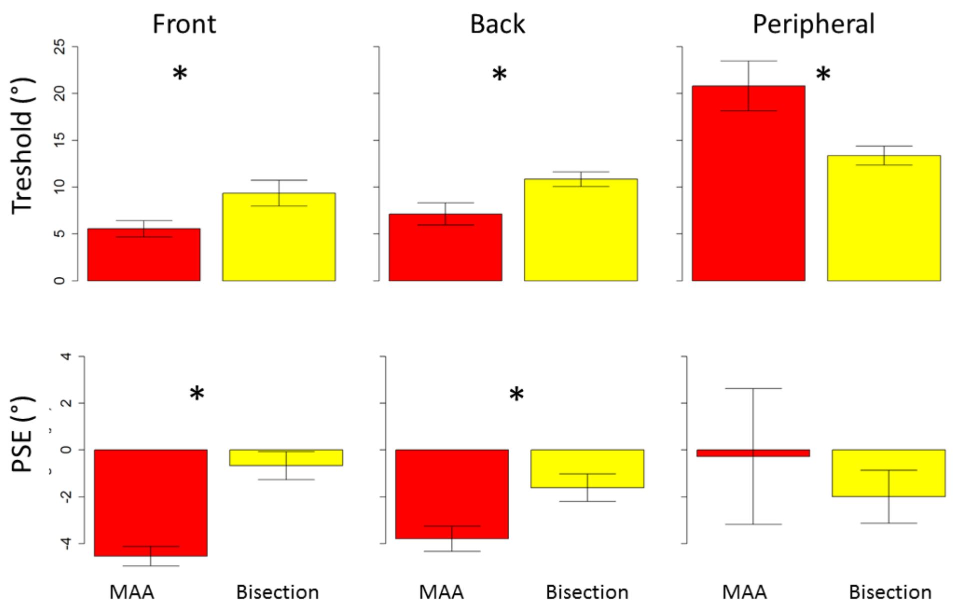

Figure 2.7 red bars report threshold (deg) for MAA task, while yellow bars refer to spatial bisection task. Upper panels show thresholds for front, back and lateral space in the left, middle and right panels, respectively. Lower panels show PSEs for front, back and lateral space in the left, middle and right panels, respectively. Error bars represent ±1 standard error of the mean. * indicates a significant difference at $p<0.05$.

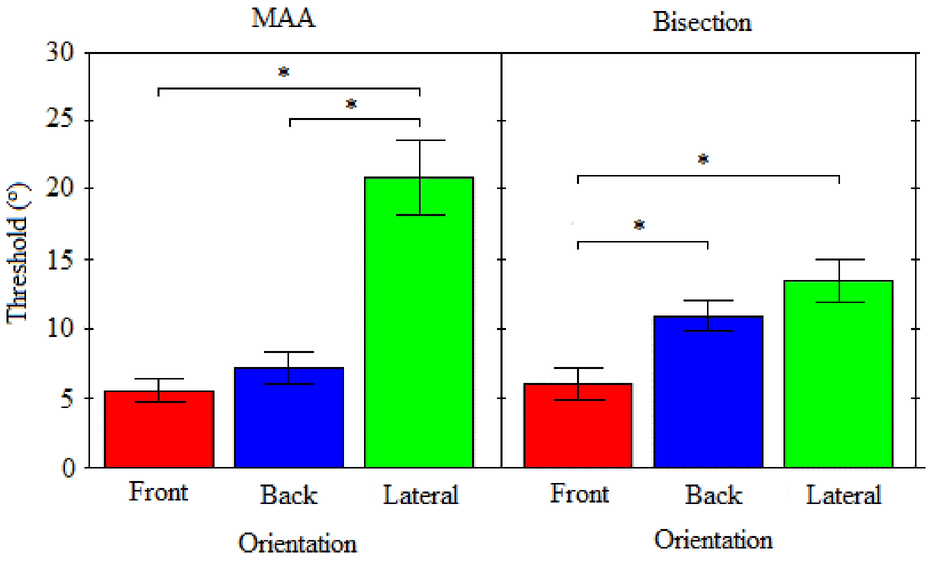

Figure 2.8 for bisection data obtained with the midpoint at 0° only. Red bars represent frontal space, blue bars represent back space and green bars represent lateral space. MAA thresholds are shown in the left panel, and bisection thresholds are shown in the right panel. Error bars represent ±1 standard error of the mean. $*$ indicates a significant difference at $p<0.05$.

compared them with the MAA thresholds. (Figure 2.9)shows mean thresholds and PSEs for MAA and bisection tasks in the upper and lower panels respectively, for front, back and lateral spatial regions, considering bisection data with the midpoint at 0° only. A repeated-measures ANOVA on the threshold values with spatial region (front, back and lateral) and midpoints between the references (4.3°, 0°, +4.3°) as within-subjects factors showed main effects of spatial region ($F_{(2,34)} = 5.2$, $p = 0.01$, ges = 0.07) and midpoint ($F_{(2,34)} = 6.1$, $p < 0.01$, ges = 0.03). The same analysis on the PSEs showed a main effect of midpoint ($F_{(2,34)} = 22.1$, $p < 0.01$, ges = 0.2). For the midpoint at 0°, a repeated-measures ANOVA was conducted on the threshold values with within-subjects factors spatial region (front, back and lateral) and task (bisection and MAA). There was a significant interaction between spatial region and task ($F_{(2,34)} = 9.5$, $p<0.01$, ges = 0.12). For front space (Figure 2.9, left panel) thresholds did not differ significantly for the MAA task (red bar) and for the bisection task (yellow bar) ($t_{(17)} = 0.3$, $p = 0.7$). For back space (Figure 2.9, center panel), the threshold was lower for the MAA task than for the bisection task ($t_{(17)} = 2.2$, $p = 0.04$). The opposite pattern was observed in lateral space (Figure 2.9right panel), for which threshold was higher for the MAA task than for the bisection task ($t_{(17)} = 3.1$, $p<0.01$). The same analysis on bias showed no significant effects (all $p > 0.05$).

2.2.3 Conclusions of the experiment

This experiment was designed to understand if the peripheral is differently represented respect the frontal and back spaces. Indeed, the different sensory information and the higher plasticity of hearing and vision, when used in this space, could lead the brain to treat differently the peripheral portion of space.

Our results suggest that the 3 spaces considerated are differently represented on the base of sensory input available. More specifically, we confirmed the different representation of complex scene (i.e. bisection task) presented in the frontal and back space, by showing that the presence of vision improves the representation of frontal space compared to the representation of the back space. Moreover we showed that representation of the peripheral space is degradated compared the frontal space while it is similar to the back space. Interesting, comparing the 2 tasks across spaces, we found that the 3 spaces are represented by using different frame of references. Indeed we found a significant difference between tasks in the frontal space when all reference positions were included, but not when only the midpoint at 0° reference position was included, suggesting that we are able to use both frame of references in the frontal space. This result may reflect the role vision plays in calibrating spatial hearing.

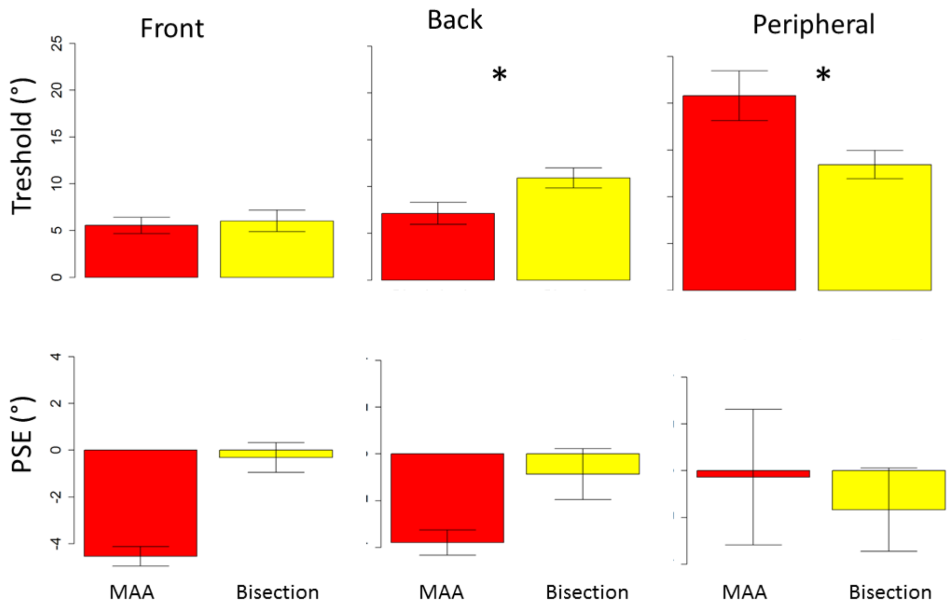

Figure 2.9 red bars report threshold (deg) for MAA task, while yellow bars refer to spatial bisection task. Upper panels show thresholds for front, back and lateral space in the left, middle and right panels, respectively. Lower panels show PSEs for front, back and lateral space in the left, middle and right panels, respectively. Error bars represent ±1 standard error of the mean. * indicates a significant difference at $p<0.05$.. Note that data for the MAA task are the same as shown in Figure 2.7

The bisection thresholds with the midpoint at 0° for front space were similar to the MAA thresholds, resembling previous results. Vision is most precise for stimuli presented directly in front, probably leading to better calibration of hearing in this region. Conversely, for back space with the midpoint at 0°, bisection thresholds were higher than MAA thresholds, perhaps indicating that lack of vision in the back leads to poorer performance in this space. Finally, this experiment adds to the previous knowledge the notion that, differently from front and back spaces, the peripheral space can be represented only adopting an allocentric reference frame, probably because the cone of confusion does not permit to use the body as reference to localize the sounds location. Our data extend previous findings on spatial perception supporting a difference between the internal representations of auditory space in the front, back and peripheral.

2.3 Exp3: The third dimension: depth

It is known that auditory spatial representation of auditory stimuli is affected by different factors, as the kind of sound and its reverbeation. Sound reverberation affects mostly the perception of distance. In this experiment, we investigated the abilities of normally-sighted, normally-hearing participants to localize the distcance of an auditory stimulus relative to two other sounds. The first aim of the experiment was to use the Virtualization techniques to investigate auditory distance bisection in anechoic and reverberant rooms for speech, noise and click stimuli. Previous auditory distance studies have measured the ability to localize the distance of a single sound on each trial for normally sighted or blind participants Kolarik et al. (2013, 2017) or to judge (discriminate) which of two successive sounds was more distant for normally sighted Kolarik et al. (2013) or blind participants. Spatial-bisection tasks are generally more difficult than single-interval localization or two-interval discrimination tasks, as they require judgment of the relative positions of three sound sources, and also the representation of the sources in auditory space has to remain in memory over the full duration of the task Gori et al. (2014). The current study extends previous studies of azimuthal bisection judgmentsTonelli et al. (2015); Vercillo et al. (2018) to the distance dimension, by investigating the accuracy of spatial distance bisection judgements made by participants with normal vision and hearing in anechoic and reverberant virtual rooms, for speech, noise and click stimuli. The second aim of the experiments was to investigate whether stimulus type affected distance bisection judgements. Speech is a familiar stimulus, and by comparing the perceived production level of speech with the signal level at the ear, participants are able to estimate how far away a talker is with generally greater accuracy than for unfamiliar stimuli such as noise. It was hypothesized that distance bisection would be better for speech than for a noise or click stimulus, as a result of participants' familiarity with the production level of conversational speech.

2.3.1 Method

The simulation methods to generate the virtual environments were similar to those used previously by Kolarik et al. for assessing absolute auditory distance perception and distance discrimination for blind and sighted controls 11,12,17,20,21. In these studies, the direct sound component was convolved with acoustical impulse responses obtained from publicly available head-related transfer functions (HRTF) to externalize the stimuli. In the current study, the realism of the simulation was increased by convolving the sound reflections with appropriate HRTFs as well as the direct sound component, as for methods used previously to simulate listening in virtual rooms 28-30. A room measuring 9 (length) x 5.4 (width) x 2 (height) m was simulated using an image-source model (ISM) 32. The simulated room was either reverberant, so that both level and DRR cues were available, or anechoic, so that only the level cue was available. The reverberation time of the reverberant room, T60 (the time taken for the overall sound level to reduce by 60 dB) was 400 ms. Binaural room impulse responses (BRIRs) between the virtual sound source and the virtual participant's head were generated using the ISM, which calculated each ray path between the simulated sound source and the virtual participant's head. For every ray, the angle of incidence at the simulated head was utilized to identify an appropriate head-related impulse response (HRIR) for each ear, that was selected from a database of publicly available KEMAR manikin recordings 33. Each HRIR was delayed and scaled according to the ray path length and absorption characteristics of the room surfaces from which the ray reflected. The HRIRs were then added to generate a BRIR, which was convolved with a sound stimulus to produce a virtual sample of the sound at the participant's ears. The virtual stimuli were presented at a height of 1 m at 0° azimuth and at 0° elevation. The center of the simulated participant's head was 1 m from the shorter wall, at the midline of the wall, at 1 m height, facing directly into the room (Figure 2.10). Stimuli were speech, broadband noise, or clicks. The speech was the British English phrase "where am I", spoken by a male at a conversational level. Its duration was 850 ms and it was sampled at 22.05 kHz, giving an upper frequency limit just above 11 kHz, matching a previous study involving room simulation to investigate binaural enhancement processing. Click stimuli consisted of a delta signal sampled at 22.05 kHz. The noise frequency range was 0.6-11 kHz and its duration was 500 ms including rise/fall times of 10 ms, sampled at 22.05 kHz. Three sounds were presented on each trial. The first and third were reference sounds and the second was the probe. The two reference sounds were presented at mean virtual distances of 2 and 7 m, and the distances were either fixed or were jittered randomly from trial to trial by ± 0.1 m, keeping the difference constant at 5 m. Jittering was included to discourage judgments based on the absolute distance of the probe, rather than its distance relative to the reference sounds. The 12 probe distances were 2.4, 2.8, 3.2, 3.6, 4.0, 4.4, 4.8, 5.2, 5.6, 6, 6.4, 6.8 m. The virtual distances of the references and probe and the room reverberation time were chosen following pilot testing to achieve appropriate task difficulty. The task is described later. In a given block of trials, a single stimulus type (speech, noise, or click) and room type (anechoic or reverberant) was used. In each block there were 120 trials, with 10 repetitions of each probe distance. Blocks were presented in a randomized order. Data collection occurred over one or two sessions lasting in total approximately 2 hours and 30 minutes, including breaks. Three sounds were presented on each trial. The first and third were reference sounds and the second was the probe. The two reference sounds were presented at mean virtual distances of 2 and 7 m, and the distances were either fixed or were jittered randomly from trial to trial by ±0.1 m, keeping the difference constant at 5 m. Jittering was included to discourage judgments based on the absolute distance of the probe, rather than its distance relative to the reference sounds. The 12 probe distances were 2.4, 2.8, 3.2, 3.6, 4.0, 4.4, 4.8, 5.2, 5.6, 6, 6.4, 6.8 m. The virtual distances of the references and probe and the room reverberation time were chosen following pilot testing to achieve appropriate task difficulty. The task is described later. Testing occurred within a quiet room using Sennheiser HD 280 PRO headphones. Stimuli were generated using a custom-written MATLAB (Mathworks, Natick, MA) script with a response interface on an Asus AA185 computer with a 64-bit Realtek High Definition sound card. 15 participants took part (7 females, mean age 36 yrs, range 28-50 yrs.) All participants had normal or near-normal hearing, as measured using the procedure described by the British Society of Audiology 31. Pure-tone average (PTA) better ear hearing thresholds across 0.5, 1, 2, 4, and 8 kHz were less than or equal to 25 dB HL. The tenets of the Declaration of Helsinki were followed. All participants provided informed consent, after an explanation of the nature and possible consequences of the experiments. Ethical approval was given by the Anglia Ruskin Research Ethics Panel. All participants were blindfolded before entering the experimental room and during testing. Participants were instructed to imagine themselves being seated in a rectangular room. They were told that they would hear three sounds appearing to originate from loudspeakers positioned at various distances away from them. The inter-stimulus interval was 500 ms. The first and third sounds were presented at the virtual reference distances in a randomized order, so that the first sound was either at 2 m and the third at 7 m or vice versa. The second sound was presented at a distance that was randomly selected from the possible probe distances. The task was to verbally report whether the second sound was closer in distance to the first or third sound. The answer was recorded by the experimenter using the response interface. Participants received no feedback, and no limits were imposed on response time.

2.3.2 Results

The probability of a response that the second sound was closer to the farther sound was calculated for each probe distance. For each participant and condition, a psychometric function was calculated: F= @(g,l,μ,v,x) g+(1-g-l)$*$0.5$*$(1+erf((x-μ)/sqrt(2$*$v$*$2))), where (μ) is the mean value of the distribution representing subject bias, the standard deviation (v) is the variation of the distribution representing the subjects discrimination sensitivity, and

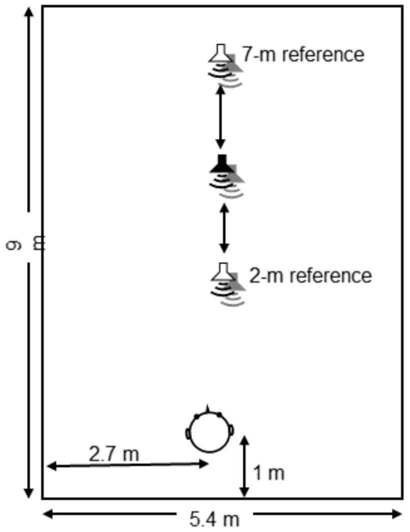

Figure 2.10 . The positions of the reference sounds are shown by white loudspeakers, and the position of the probe sound is shown by a black loudspeaker. Note that the positions of the reference sounds were jittered from trial to trial (not shown).

guess rate (g) is an additional parameter representing the subjects fallibility (i.e. potential inability to ever reach 100%performance)at each end of the distribution/stimulus spectrum 34. The standard deviation *sigma* of the fit, which provides an estimate of the slope of the psychometric function, was taken as the estimate of threshold. The Point of Subjective Equality (PSE) was estimated as probe distance leading to a response probability of 0.5. As not all subjects could perform all conditions (3 participants could not perform the click condition due to the difficulty of the task), a repeated-measures Analysis of Variance Model was fitted to the threshold and PSE values using the lmPerm package in R, with within-subjects factors room type (reverberant and anechoic) and stimulus type (speech, noise, and click). Significant effects were further analyzed using a two-sample permutation Welsh's t test (number of resamples B = 1000) implemented by the perm.t.test function of the package Deducer in R. This function computes t value from the t test comparing raw two samples. Then for N = 1000 bootstraps calculate t value comparing one pair of surrogate samples obtained by mixing elements of the raw two samples. Then the final p value of the test is computed by comparing t value corresponding to raw data with the distribution of 1000 t values obtained by surrogates. Therefore, no degrees of freedom are provided by this function. We considered $p<0.05$ as significant. For the thresholds *sigma* there were main effects of room (F = 41, p<0.01) and stimulus type (F = 60.6, *p* <0.01) and a significant interaction (F = 7.57, p<0.01). However, the general pattern of the results was similar for the anechoic and reverberant rooms (Figure 2.11left and right panels, respectively). There were no significant differences in threshold for the speech and noise stimuli in either room (anechoic: t = 0.61, p = 0.64; reverberant: t = -0.54, p = 0.59), while performance for clicks was significantly worse than for speech in both rooms (anechoic: t = -2.88, p<0.01; reverberant: t = -14.28, p<0.01) and for noise in both rooms (anechoic: t = 4.16, p<0.01; reverberant: t = 12.22, p<0.01). For the clicks, thresholds were significantly lower for the anechoic room than for the reverberant room (t = -6.01 p<0.01), the same was true for noise stimuli (t = -3.6, p<0.01). Thresholds did not differ significantly between the anechoic and reverberant rooms for speech (t = -1.4, p = 0.1).

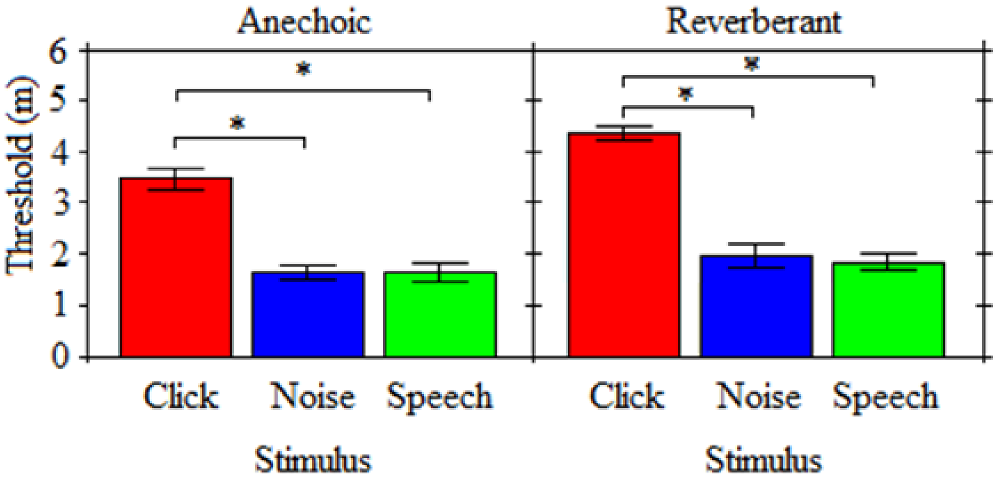

Figure 2.11 Bars represent PSE for click (red bars), noise (blue bars) and speech (green bars) stimuli. Error bars represents standard errors. The dashed line shows the average midpoint between the two reference sounds.

For the PSEs there were significant effects of room (F = 10.70, p<0.01) and stimulus type (F = 51.69, p<0.01) but no significant interaction (F = 1.97, p = 0.14). (Figure 2.12) shows averaged PSEs for speech, noise and click stimuli for anechoic and reverberant rooms (left and right panels, respectively). The average PSEs for speech (anechoic: 3.9 m, reverberant: 3.7 m) and noise (anechoic: 4.1 m, reverberant: 3.7 m) were closer to the participants than the average midpoint between the two reference sounds (4.5 m, dashed line in Fig. 3), indicating that the participants underestimated the distance to the midpoint. However, the average PSEs for the click stimulus (anechoic: 5.7 m, reverberant: 4.9 m) were farther than the midpoint, indicating that participants overestimated the distance to the midpoint. No significant differences were found between PSEs for speech and noise stimuli in either room (anechoic: t = -1.4, p = 0.1 reverberant: t = -0.4, p = 0.6), while PSEs for clicks were significantly larger than for speech (anechoic: t = -6.4, p<0.01; reverberant: t = -4.2, p<0.01) and for noise sounds (anechoic: t = 5.9, p<0.01; reverberant: t = 4.2, p<0.01). PSEs for the clicks were significantly smaller in the reverberant than in the anechoic room (t = 2.2, p<0.03). There were no significant differences between virtual rooms for speech PSEs (t = -1.3, p = 0.8) or noise PSEs (t = 2.6, p = 0.1).

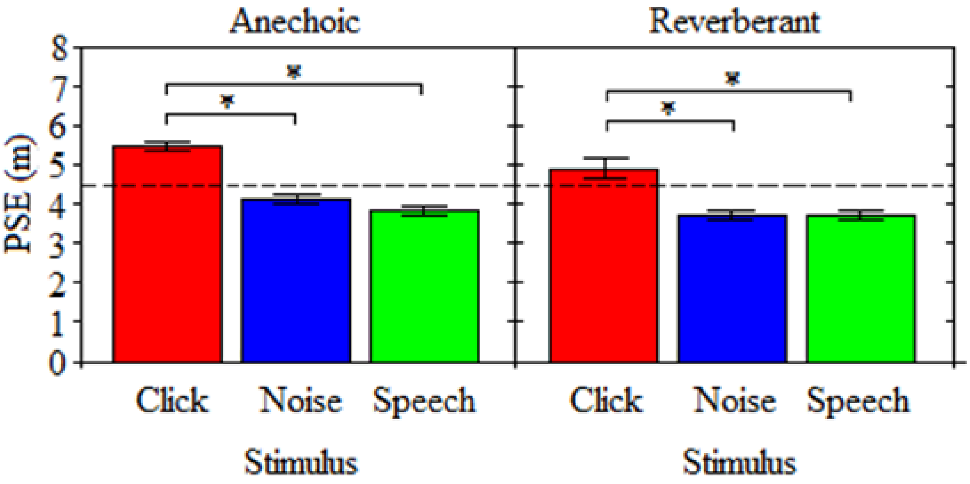

Figure 2.12 Bars represent mean thresholds for click (red), noise (blue) and speech (green) stimuli.Thresholds for the anechoic and reverberant virtual rooms are shown in the left and right panels, respectively. Error bars represent ±1 standard error of the mean. * indicates a significant difference at p<0.05.

2.3.3 Conclusions of the experiment

Summarizing we found that for clicks, bisection thresholds were significantly lower in an anechoic than in a reverberant virtual room, suggesting that room reverberation time did not affect thresholds for speech and noise stimuli. Moreover, we found that compared to speech and noise, bisection thresholds for click stimuli were significantly higher in both virtual rooms, while speech and noise thresholds were not significantly different for the two virtual rooms. Regarding PSE, the true point of equality was underestimated for speech and noise stimuli, while for clicks it was overestimated and this overestimation was more evident for clicks in the anechoic room than for the reverberant room, while the PSEs for speech and noise were the same for the two rooms. Finally, PSEs for click sounds were significantly farther from the objective point than for speech or noise in both virtual rooms, while speech and noise PSEs were not significantly different in the two rooms.

2.4 Interim conclusions

The experiments presented in the previous paragraphs have the common goals of exploring if different portions of space are differently treated by the brain and if this spatial representation is due to the different availibility of visual and audio modalities. Bisection task and MAA, testing respectively allocentric and egocentric frame of reference were used in frontal, rear and lateral space. With this configuration, we were able to test the contribution of senses in representing these spaces and the reference frame used to build a spatial map. We found that people perform the bisection task better in the frontal space compared to the back, suggesting an important role of vision in building a spatial metric. Important, MMA were similar in the 2 spaces suggesting that spatial acuity not differ between spaces. Moreover, we found that MAA is performed worse than bisection in the lateral space. This is an interesting result; indeed, MAA is easier than bisection task, anyway, to be resolved it requires egocentric frame of reference. The fact that in the lateral space, MAA is performed worse than bisection task, suggests that this space need allocentric reference frame to be represented. In the rear space subjects performed better in the MAA suggesting that this space need egocentric reference frame. The reason of this result could be due to the fact that the lack of vision did not allowed the development of allocentric reference frame. Finally, in the frontal space both reference frame can be used, however, subjects performed better in the egocentric reference frame. Spatial metric was also tested in longitudinal dimension with 3 different sounds (speech, noise, click) in 2 different virtual rooms (reverberant and anechoic). Results showed that subjects performed worse in the click condition in both room and in the clicks condition, subjects reported larger overestimation of the position of the second sound when delivered in the anechoic room than in the reverberant room. The PSEs for speech and noise were the same for the two rooms. Room reverberation did not affect thresholds for speech and noise stimuli, however for clicks, thresholds were significantly lower in the anechoic than in the reverberant room. This seems surprising, as an internal representation of the distance to a sound source is generated by combining information from the available auditory cues and reverberation is usually a beneficial cue for auditory distance judgements. In conclusion, these series of experiments enrich previous knowledge on spatial cognition, by showing that space around the body is split in several portions differently treated by the brain. More specifically, we showed that this spatial parcelization is due to the different availibility of sensory information across the body space.

Chapter 3

Audio visual interaction in spatial localization in blind and sighted individuals

A congruent representation of the external world has to be provided by the different senses, so that the objects registered by more than one modality can be reliably localized and identified. In the case of vision and hearing, this means that activation of a specific region of the retina corresponds to a particular combination of monaural and binaural localization cues values. Because most animals can move their eyes, that relationship is not fixed. Consequently, the neural processing and perception of auditory spatial information is also influenced by the direction of gaze Bulkin and Groh (2006); Zwiers et al. (2001). Indeed, central nervous system combines inputs across the senses to enhance the detection, localization and discrimination of stimuli and speed up reactions to them. This is an example of a more general phenomenon by which the central nervous system can combine inputs. Cross-modal interactions are helping when conflicting information is provided by different senses. However, when the visual and auditory signals no longer match, as in the 'McGurk effect'Mcgurk and Macdonald (1976); they can interfere each other. Despite, sound sources can obviously be localized on the basis of auditory cues alone, localization accuracy improves if the target is also visible to the subject Shelton and Searle (1980); Stein (1989)(Shelton e Searle 1980; Stein et al. 1989). Human observers are used to localize events in the world by using complex mapping of sensory signals, from multiple modalities, that leads to a perceptual judgment. Usually, events in the environment provide consistent cues to spatial location; when we grasp something, like a bell, vision, hearing and tactile stimuli are all located in the same spatial position. However, some times, stimuli in the environment do not show this spatial consistency. For example, when we watch a movie on the cinema's screen, the visual information is located on the screen whereas the auditory information often comes from loudspeakers located in another position. Nevertheless, we do not notice this incongruence and we perceive the sound as originating from the location of the visual stimulus (e.g. the moving lips of a face or the noise of a car). This is an example of "visual capture" in which the visual information for spatial location dominates completely the conflicting auditory informationPick et al. (1969); Welch and Warren (1980) .Knudsen (1995) and his colleagues have shown in the barn owl that vision dominates audition when these two sources of information are artificially put into conflictBrainard and Knudsen (1998); Knudsen (1995).Juvenile barn owls, whose auditory cues to the location of a sound are altered (with a monaural earplug) or whose visual cues to object location are altered (with displacing prisms), recalibrate the relationship between sight and sound, with vision dominating audition Battaglia et al. (2003). This phenomenon of visual capture is known as "ventriloquism effect". This effect support the idea of a visual dominance over audition in spatial tasks, due to the superior spatial acuity of vision compared with audition. Instead, in temporal domain, it has been suggested that auditory system has superior acuity. For this reason, in temporal task, the interaction between vision and audition is dominate by hearing. Recanzone (2003)tested the interactions of visual and auditory stimuli in a temporally based task in normal human subjects. They showed that the auditory system can strongly influence visual perception and this influence is strongly dependent on the disparity in temporal rate between the two stimulus modalities. Important, this influence is independent of the spatial location, spectral bandwidth, and intensity of the auditory stimulus. Two theories predict how visual and auditory information are weighted when signals from different modalities are in conflict. According to one theory, the signal that is typically most reliable dominates in a winner-take-all competition, whereas the other theory (maximum likelihood estimation) proposes that perceptual judgments are based on a weighted average of the sensory signals in proportion to each signal's relative reliability.Battaglia et al. (2003)tested this two theories in a visual capture task. They examined the extent to which subjects use visual and auditory information to estimate location when the visual signal is corrupted by noise of varying amounts. When a greater amounts of noise were added to the visual signal, subjects tended to use auditory information more and more. They concluded that both models are partially correct and they suggested that a hybrid model might provide the best account of subjects' performances. The influence of the visual system on the spatial location of auditory (and somatosensory inputs) is probably due to the high spatial acuity of the visual system compared with the other two sensory modalities. Sound localization Localizing a sound source is a highly complex computational process that takes place within the brain. Differently from vision, the ability to localize sounds in space depends on anatomical and physiological properties of the auditory system as well as on behavioral cues. The auditory space cannot be mapped onto the cochlea in the inner ear in the same way of vision in the visual area; the direction of a sound source has to be inferred from acoustical cues generated by the interaction of sound waves with the head and external ears Blauert (1997). The separation of the ears on either side of the head is key to this, as sounds originating from a source located to one side of the head will arrive at each ear at slightly different times, producing, so, a gap between when the sound reach the left and right ear (ITD). This is the dominant binaural cue for low frequency sound source localization. Moreover, by shadowing the far ear from the sound source, the head produces a difference in amplitude level at the two ears (ILD). This is an important cue for high frequency sound Macpherson and Middlebrooks (2002); Middlebrooks (2015). The level of the sound is also altered by the direction-specific filtering by the external ears, giving rise to spectral localization cues. By themselves, each of these spatial cues is potentially ambiguous and is informative only for certain types of sound and regions of space. For these reason, it is difficult, for the human brain, to disambiguate the position of the sound placed in front of or behind the body. This spatial perceptual ambiguity is known as the cone of confusion Wallach (1938), an imaginary cone extending outward from each ear, representing sound source locations producing the same interaural differences. When the binaural information correlates equally well with two opposite spatial locations, it is possible to incur in reversal errors Carlile et al. (1997); Scharine and Letowski (2005). In this specific condition, the estimation of the sound source location is reported in the opposite direction to the actual sound source location. Despite their significant role in horizontal localization, binaural cues are less efficient for vertical localization or front–back differentiation. Front–back (FB) and back–front (BF) errors are the most common reversal errors. However, they are rare for open ear conditions and are most frequent for sound sources located on or near to the median plane Makous and Middlebrooks (1990). Usually, front–back errors dominate back–front errors, but their proportion depends on various factors, such as the visibility of the sound sources Chasin and Chong (1999). Monaural cues are more powerful in differentiating between specific positions on the surface of the cone of confusion, as they do not depend on the presence of two ears. They result mostly from sound absorption by the head and the outer ear (pinna) Butter et al. (1989); Lopez-Poveda and Meddis (1996); Musicant and Butler (1984). Several studies have reported that localization error of static sounds is more accurate in the frontal space, at head level, while error increased in the regions behind the head (Oldfield and Parker, 1986). early blind (EB) individuals (approximately half of those tested) can localize sound sources in the horizontal plane with a high degree of accuracy when having to do so with one ear occluded Gougoux et al. (2005); Lessard et al. (1998). EB have been shown to have better sound source discrimination abilities in peripheral auditory space near the interaural axis Röder et al. (1999); Voss et al. (2004a), where binaural cues are insufficient to resolve whether a sound source lies in front or behind the axis and where spectral cues can help to resolve this ambiguity. In the next paragraphs, I will present three experiments testing the effect of visual deprivation in localizing stimuli delivered around the body. When vision is momently absent, movement can help in localize simple sound. This is shown in the first experiments, where we found that discriminating front from back sound is a hard task, especially at foot level. In the second experiment, we were aimed to better understand spatial hearing around the legs, where visual, tactile and audio stimuli are not always integrated in the same spatial position. We were especially interested in understanding the influence of visual experience in this space. To do so, we tested blind and sighted people in a front back discrimination task around legs. In the last section of this chapter, I will show that not only vision influence spatial perception. Indeed, preliminary results suggest that in case of absence of vision, people use time to infer space.

3.1 Exp1: The role of body movement in representing auditory spaces

In this study, we investigated the influence of visual and motor localization vs verbal localization of sounds in four different body regions: front, back, around chest and around feet. As seen before, several cognitive and perceptual factors influence spatial cognition and sound localization. With this goal in mind, subjects were requested to perform an audio perception task in the frontal and back zone, at high and low level, and giving a motor or verbal response. Firstly, we investigated how front and back auditory spaces are perceived; to do this, we manipulated sound location by delivering stimuli in the frontal and rear space to investigate the influence of visual and motor experience in space where their are not naturally available. To investigate whether frontal and rear auditory space differ for upper, where vision dominates, and lower body portions, where feet produce sounds during walking, we manipulated sound elevation, by delivering stimuli around the chest area and around the foot area. To investigate the influence of movement on audio perception, subjects had to report the sound position with a body movement, in one condition, or by giving a verbal answer in another condition. Finally, we investigated whether sound features could influence the localization of auditory stimuli by presenting both dynamic and static sounds. Results suggest that auditory perception is different for different body portions and modulated by actions. These findings suggest that senses and actions have a different weight in representing/shaping spatial representation of auditory stimuli delivered around the body.

3.1.1 Method

Subjects Twenty-six healthy participants took part in the study (13 females: average age 25 ± 3 years and 13 males: average age 30 ± 12 years). All participants had a similar level of education (at least an Italian high school diploma, indicating 13 years of schooling). A group of 11 people (4 males: average age 27 years ± 4 and 7 females: average age 27 years ± 5) performed motor pointing tasks, while a group of 15 people (9 males: average age 30 years ± 14 and 6 females: average age 25 years ± 3) performed verbal pointing tasks. All participants confirmed they were right handed and right footed, and they had normal or corrected-to-normal visual acuity and no history of hearing impairment. All 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).

The experiment was performed in a dark room. The apparatus consisted of a circle (radius =50 cm) drawn on the floor in the center of the room (far from each wall). Participants stood at the center of the circle and remained in this position for the entire duration of the experiment. Four different positions were marked on the perimeter of the circle; two positions were placed in the frontal portion of the space at -20° and 40° respectively, two positions were placed in the back portion of the space at 160° and 220° respectively (Figure 3.1). All four positions were evaluated five times, for a total of 20 trials per condition (80 trials per participant). All subjects enrolled were assigned to one of two groups and each group performed two conditions of a sound motion localization task (Figure 3.1). The first group of subjects had to

(1) locate a dynamic sound with a motor pointing task using the foot and

(2) locate a dynamic sound with motor pointing task using the hand

The second group of subjects had to:

(1) locate a dynamic sound with a verbal response by a localization label, and

(2) locate a static sound with a verbal response by a localization label.

All conditions were divided into two randomized blocks in which the sound was delivered at high (chest) or low (foot) levels. Sound stimuli were delivered by a digital metronome (Keuwlsoft, United Kingdom) set as single pulse (with no sub pulse), intermittent sound at 180 bpm; it showed a component at 1000 Hz. All subjects confirmed that they could hear the sound clearly. The same experimenter (EAV) administered all the tasks to all subjects; she was trained to keep the velocity of the moving sound constant, so that all features of stimulus were consistent across trials, positions, conditions and groups. She moved around the circle, holding the sound source, in order to produce the sound stimuli. We adopted a metronome as stimulus, as we were interested in understanding the interaction between motor and auditory systems in representing space, and the rhythmic sound was found to activate motor system Grahn and Brett (2007). All participants were blindfolded before entering the experimental room in order to avoid side effects related to setup or room observation. During the conditions for which a motor response was required (first group), four spherical markers were placed on the subjects' hands and feet for motion tracking: one on each distal phalange of the two index fingers and one on each distal phalange of the two big toes, (Vicon Motion Systems Ltd., United Kingdom). Four other markers were placed on the four positions on the circle Figure 3.1; the markers placed on the floor represented the end point of the sound stimuli, i.e., where subjects should point. These markers were used to compute accuracy and precision. This paradigm was developed starting from the setup used inFinocchietti et al. (2017). All pointing movements were carried out on the same level of the effector used, regardless of the sound elevation (elevation did not change within condition); in order to avoid trunk torsions and to increase pointing accuracy, subjects were free to use the right or left effector. In this way, the two spaces taken into account maintained the same relationship in relation to the body space throughout all trials (i.e. avoiding torsions, the head was always aligned with the body, making frontal and back space constant in relation to body and head axes). It is important to note that, in the condition where pointing was performed with the hand, at starting position subjects were required to keep their hands on their chest (level at which the high sound was delivered). This arrangement was adopted because moving sounds within peripersonal space (PPS) modulate the motor system Finisguerra et al. (2015). Participants were instructed not to move the effector until the end of the audio motion and to keep their head straight. Each time, after pointing, subjects returned to the original central position. During the conditions for which a verbal response was requested (second group), subjects specified the sound source location by selecting it from a set of specifically labeled locations ("front-left, front-right, back-left, back-right"). When asked to localize the static sounds, the experimenter placed the sound in one of the four possible positions marked on the circle, while when asked to localize the dynamic sounds the experimenter moved the sound from the subject toward one of the four positions.

Kinematic data were post-processed and analyzed using Matlab (R2013a, The Math Works, United States), while R program (R Development Core Team, New Zealand) was adopted for the statistical analysis. Localization error and spatial precision (on x and y-axes) were computed for each participant and for each spatial position. The x- and y-coordinates in relation to subject position were obtained by a custom made program in Matlab. Localization error (also called error) was calculated as the distance (in cm) between the end-point position signaled by the participant and position of the reference marker placed on the circle. The error was averaged based on the number of trials per position and on the number of participants. To better explore the meaning of the localization error, we calculated bias separately on x-and y-axes by subtracting the coordinates of the reference marker from the coordinates corresponding to the average end-point positions signaled by the participants. The precision on x-and y-axes was calculated as standard deviation for each point, averaged among subjects. We supposed that points with the same longitudinal position in relation to the body were homogenous in localization error (as they share the same area as the body). A t-test confirmed our hypothesis, allowing us to group the four points into two spaces, i.e., front and back. In order to understand whether auditory space representation is influenced differently by sound elevation (around chest and around foot), effector used to point (hand, foot) and longitudinal position (front, and back space), we performed five repeated measure ANOVAs, independently considering localization error, bias, precision on x-axis and precision on y-axis. In the verbal tasks, subjects were required to indicate the end point of the sound by naming. We fitted a beta regression model for proportions of responses given by the subjects in each quadrant, therefore considering proportions as a function of sound level (high level vs. low level), longitudinal position (front vs. back space) and transversal position (right vs. left). We calculated Analysis of Deviance Tables (using Type II Wald chi-square tests) for the models using the Anova function of the car package. For significant effects, we performed post hoc comparisons using the lsmeans package , which computes and contrasts least-squares means (predicted marginal means). We adopted MVT P adjustment, which uses a multivariate t distribution. Contrasts, with $P < 0.05$ were considered as significant (P corrected are reported). The same analysis was also adopted to investigate front–back error in the motor pointing task.

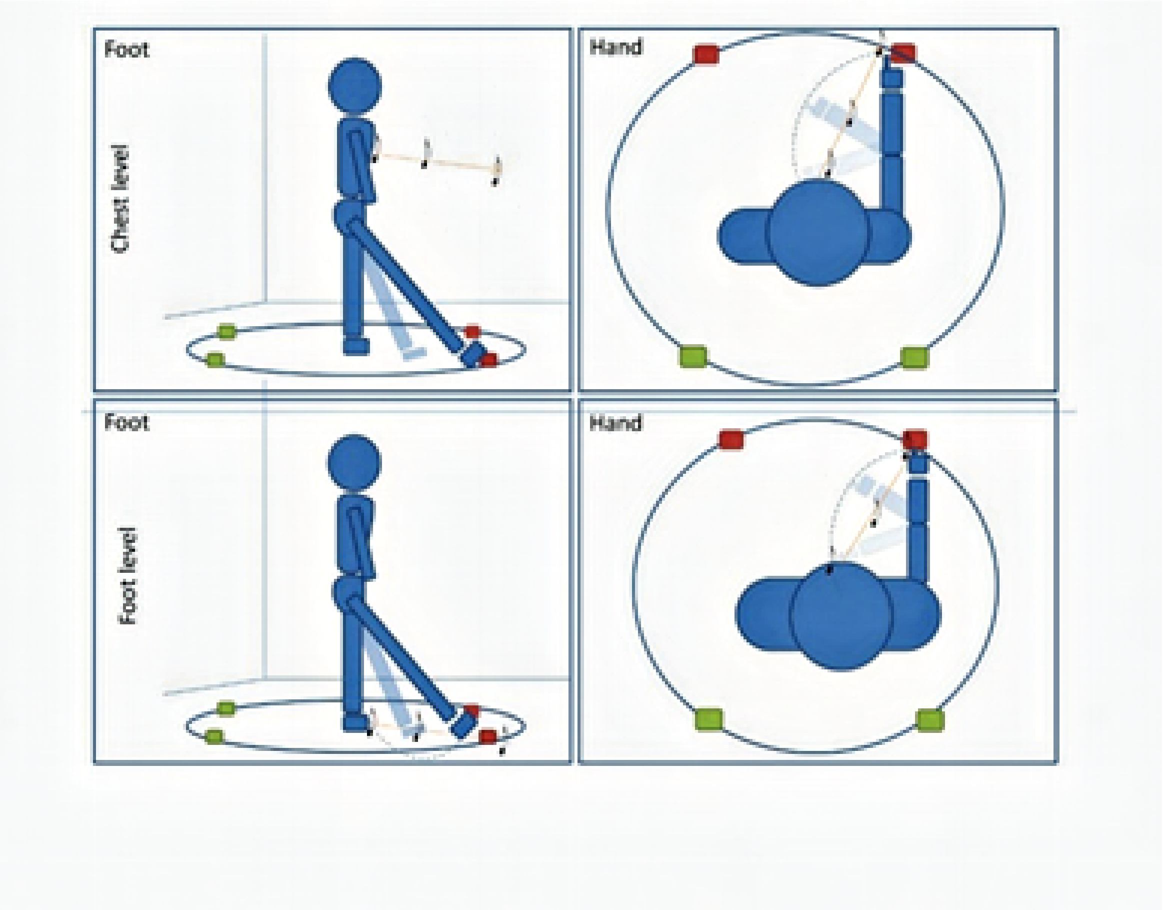

Figure 3.1 Pointing task: subjects performed four conditions of a auditory pointing task. In two conditions subjects were asked to point with (1) foot (first column)or (2) hand (second column) to the final position of a sound moving radially from the subject to one of the four positions. In the other two conditions, subjects were asked to orally locate a (1) moving or (2) static sound delivered at one of the four positions on the circle (red for frontal point, green for back point). For all conditions, sounds were delivered at high (chest, first line) level and at low (foot, second line) level.

3.1.2 Results

Three models were used to analyze our data. For data regarding the motor point, we adopted an Anova on localization error and anova on bias on x- and y-axes. Data from every tasks were analyzed with a beta regression on proportion of responses. All model showed a particular salience of the back space, with difference between high and low space. While in the low space subjects localized frontal sound in the back, displaying a great number of front–back errors; in the high space, the front–back error was still present in the oral conditions, while in the motor condition, the error was better explained by a shift toward the back of sound perception.

Localization Errors (Figure 3.2A) reports localization error and precision (standard error for each point averaged among subjects), in x- and y-axes for the motor audio pointing. Specifically, upper and lower rows represent sound levels, chest and foot, respectively, while left and right columns represent hand and foot effectors. In each quadrant, the subject is indicated by the head at the center ($x = 0$ cm, $y = 0$ cm) and he/she is facing toward positive x-values. Black circles represent the four targets to be located, while colored squares denote the average of locations actually located (indicated by numbers): red and green squares refer to the front and back longitudinal spaces, respectively. Subjects were generally more accurate (smaller localization error) in the back space than in the frontal space [$t_{(10)} = 3.5$, $P = 0.006$] and in the space around chest, than the space around foot [$t_{(10)} = 5.4$, $P = 0.0003$]. However, anova on localization errors showed that sound elevation (chest vs. foot level) significantly influences sound localization on the longitudinal plane (front vs. back) [$F(1,10) = 21$, $P = 0.001$]. Indeed, when the sound was delivered at chest level, subjects showed similar error in localizing sounds coming from both the frontal and back space [$t_{(10)} = 0.9$, $P = 0.7$], while, when the sound was delivered at foot level, there was greater localization error in the frontal space than in the back space [$t_{(10)}= 4.8$, $P = 0.001$]. No significant localization errors were observed when the sound was presented at chest level (squares are almost superimposed on circles in the upper line in(Figure 3.2A). Contrarily, at the foot level, frontal sounds were mostly perceived as coming from the back and a strong localization error emerged (lower line in (Figure 3.2A). (Figure 3.2B) reported the average error, considering frontal and back regions. Interestingly, precision was equal for different sound elevations, on both: the x-axis [$F_{(1,10)} = 1.8$, $P = 0.2$] and the y-axis [$F_{(1,10)} = 2.6$, $P = 0.1$].

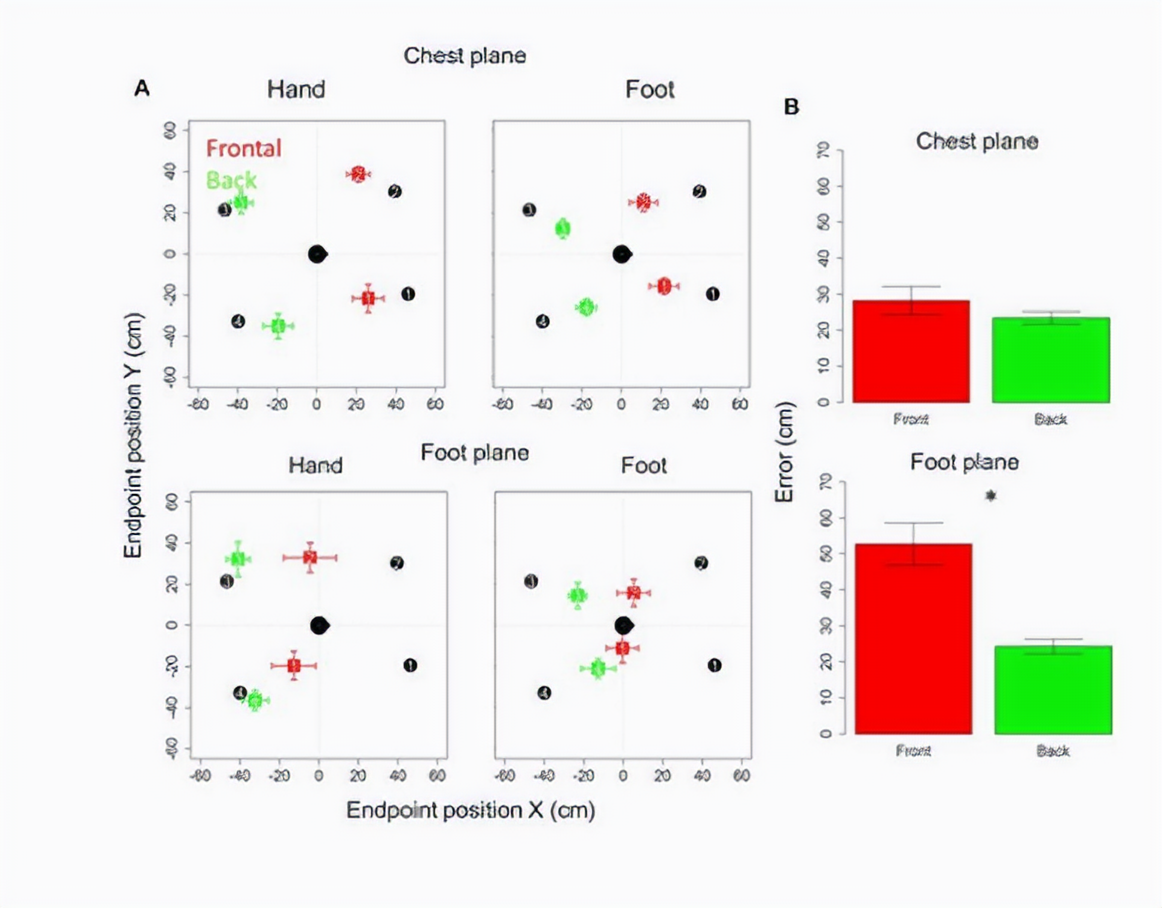

Figure 3.2 Bias and localization error in motor pointing task: (A) upper and lower rows represent sound levels: high and low, respectively; left and right columns represent the effector used: hand and foot, respectively. In each quadrant, the subject is indicated by the head at the center facing toward positive x-values. Black circles represent the four positions to be located, while colored squares denote the average of locations actually located: red and green squares, respectively, refer to the front and back longitudinal spaces, respectively. As can be seen, there is greater bias at foot level (red squares are shifted toward the back), while at chest level the bias disappears (green dots are almost superimposed on black dots). (B) Reports localization error (distance in cm between the end-point position signaled by the participant and position of the reference marker placed on the circumference). As can be seen, similar localization in front and back space is reported for sounds delivered at chest level, while greater localization error in the frontal space appears when sounds are delivered at foot level. Significant differences are illustrated ($* P < 0.05$).

In order to test the role of the effectors (hand or foot) on the audio spatial bias, we carried out the task twice, asking to the subjects to point with either the hand or foot. The localization error on the longitudinal plane (front vs. back) was influenced by the effector used and sound level [$F_{(1,10)} = 8.3$, $P = 0.02$]. (Figure 3.3)compares error in localizing frontal (red bar) and back sound (green bar), when pointing with the hand (left column) and with the foot (right column), at both sound elevations, chest level (upper line) and foot level (lower line). As can be seen, with sounds delivered at chest level, subjects were similarly accurate in localizing frontal and rear sounds with both effectors, hand [$t_{(10)} = 0.6$, $P = 1$] and foot [$t_{(10)} = 1.2$, $P = 1$]. At foot level, subjects displayed higher accuracy for sounds presented in the back space, when pointing with the hand [$t_{(10)} = 5.5$, $P = 0.001$] and a trend of the same pattern emerged when pointing with the foot [$t_{(10)} = 2.5$, $P = 0.1$, P uncorrected (0.03)]. This suggests, therefore, that the effector was not the main cause of the bias.

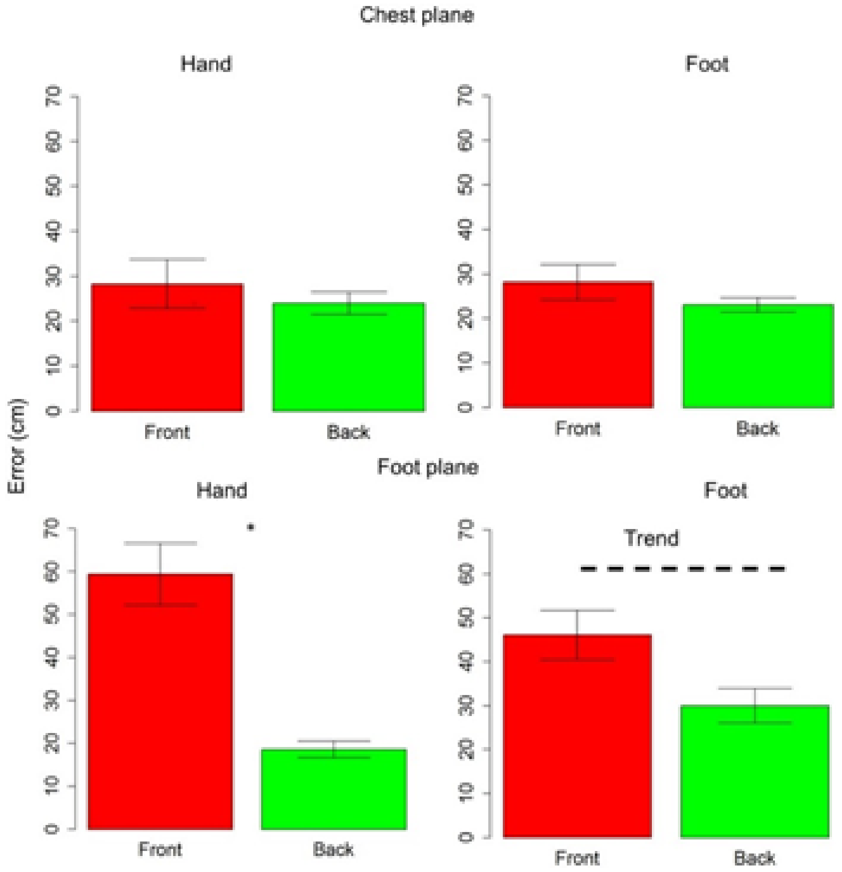

Figure 3.3 Effectors influence localization in frontal and back space at foot level: upper line shows localization error for sounds delivered at chest level, while lower line reports localization error for sounds delivered at foot level. The first column reports data for hand pointing, the second column represents pointing with the foot. The red bar refers to frontal space, while the green bar represents back space. As can be seen, at chest level subjects were similarly accurate with both effectors, in both spaces. At foot level, a significant difference between frontal and back space is reported when pointing with the hand. The same pattern (trend) is also reported when pointing with foot. Significant differences are illustrated ($* P < 0.05$).

To determine the contribution of x- and y-axes in the localization error, we performed an analysis on (i.e. perceptual bias that could lead to give always the same response, leading to high accuracy in one space and low accuracy in the other),.

Bias Anova on bias showed no differences on the y-axis (all $P > 0.05$); while on the x-axis, spatial bias emerged. The bias is specific for the frontal space [$F_{(1,10)} = 5.7$, $P < 0.001$], showing that subjects perceived frontal sound toward the back. The bias is present at foot level [$t_{(10)} = -0.7$, $P < 0.001$] and at chest level [$t_{(10)} = 7.6$, $P < 0.001$], as shown in (Figure 3.4A). Interestingly, when comparing rear space at foot and chest level, no bias is reported [$t(10) = 0.38$, $P = 1$], while when comparing chest and foot frontal spaces, a strong bias appears at foot level [$t_{(10)} = -4$, $P = 0.005$], as can be seen in (Figure 3.4B). Bias on longitudinal space is not affected by the effector adopted [$F_{(1,10)} = 3.6$, $P = 0.01$]. However, effector influences bias on sound elevation [$F_{(1,10)} = 2.22$, $P = 0.6$], showing similar results with hand and foot for sound delivered at chest level [$t_{(10)} = -0.23$, $P = 1$] and a smaller bias at foot level, when pointing was performed with the foot [$t_{(10)}= -32$, $P = 0.02$]. These data shows that localization error was mainly due to a bias on the x-axis and not on the y-axis.

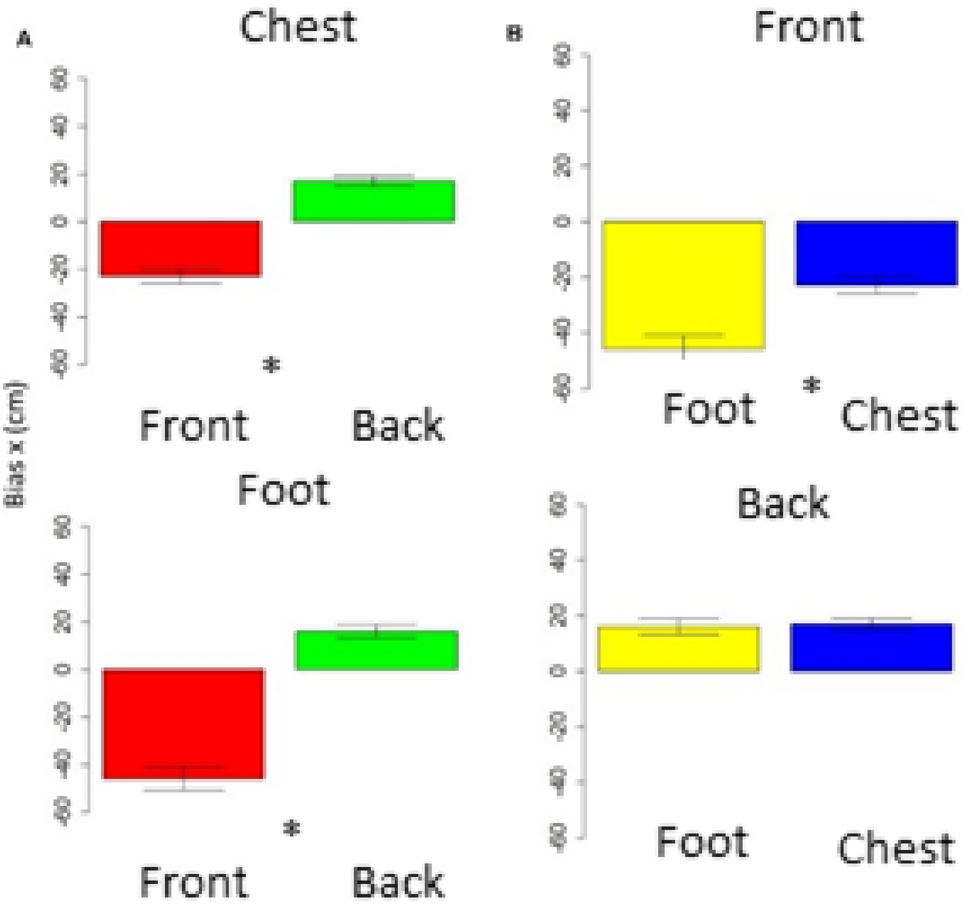

Figure 3.4 (A) Left plots compares front (red bar) and back (green bar) bias for sounds presented at high level (upper plot) and low level (lower plot). As can be seen a greater bias is present in the frontal space than in the back. (B) Right plots compare low (yellow bar) and high (blue bar) sound level, in the frontal (upper plot) and back (lower plot) spaces. As can be seen, there is a significant difference between sound elevations in the frontal space, while no difference in the back space. Significant differences are illustrated ($* P < 0.05$).

Beta Regression Model To elucidate whether the bias was due to an overturning (i.e., sound presented in the front perceived in the back) perception or to a shift toward the back of pointing (i.e., perceived as closer to the body but still in the same hemifield), we fitted a beta regression model for proportions of responses. In the motor pointing, analysis on frequencies once again showed an influence of sound elevation (chest vs. foot level) on the longitudinal plane (front vs. back) [$X^2_{(1)} = 18.40$, $P < 0.001$]. There was no differences between “Front” and “Back” responses for sound delivered at chest level [(OR) = -0.02 ± 0.01, z.ratio = -1.52, P = 0.11], while a greater number of “Back” responses were given at foot level [(OR) = 0.06 ± 0.01, z.ratio = 4.09, $P < 0.001$] (Figure 3.5). Interestingly, no differences between high and low spaces were found in the back [(OR) = -0.03 ± 0.01, z.ratio = -2.161, P = 0.03], while in the frontal space a lower number of ‘frontal’ answers were given at foot level [(OR) = 0.05 ± 0,01, z.ratio = 3.48, P = 0.0005]. Moreover, independently from elevation, transversal position (left vs. right) influences sound localization on longitudinal position (front vs. back), showing a greater number of “back” responses for sound presented on the left [(OR) = 0.09, z.ratio = 4.87, $P < 0.001$], while a greater amount of front answer for sound delivered on the right [(OR) = -0.05, z.ratio = -3.74, P = 0.0002].I

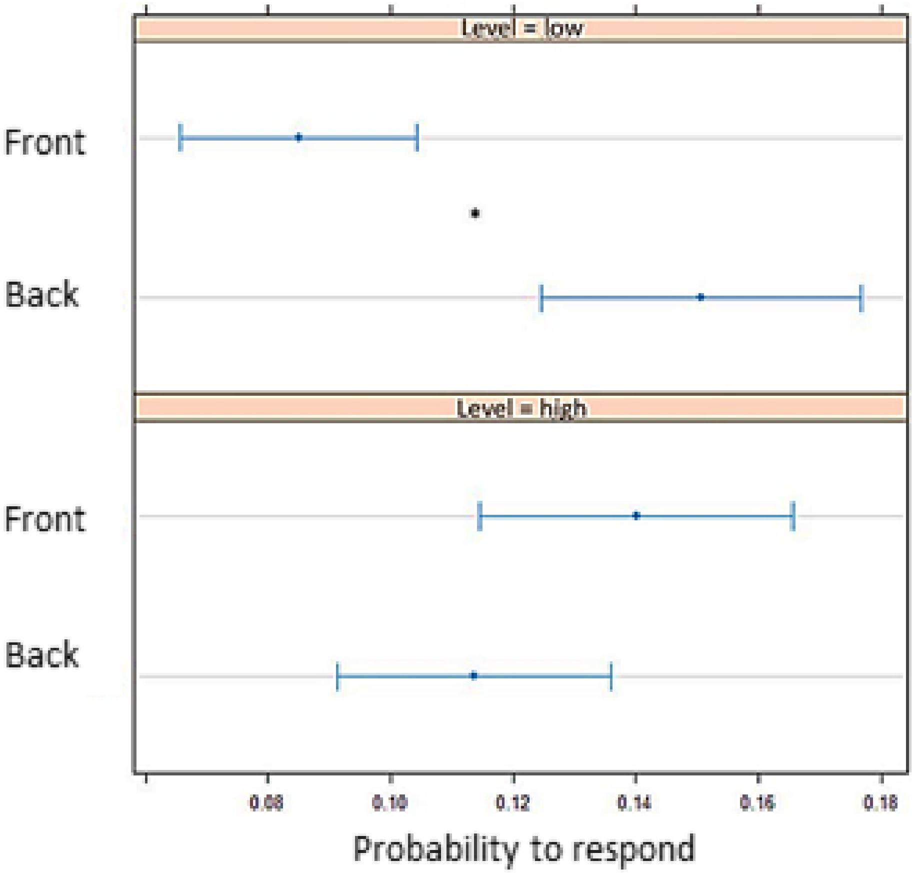

Figure 3.5 Proportion of verbal of answers in motor pointing task: the plot represents the amount of front and back answers given for sounds presented at low level and at high level. As can be seen a greater number of ‘back’ responses is present at low level, while at high level, no difference is present between the two longitudinal space. Significant differences are illustrated ($*$ P $<$ 0.05).

In order to clarify the role of the motor response on the bias, we performed the task, in another group of subjects, asking them to give a verbal, instead of motor, response (verbal condition). A greater number of ‘back’ responses was given compared to frontal position [(OR) = 0.17 ± 0.01, z.ratio = 11.8, P = <0.001]. This suggest that front back error toward the back was still present for sound delivered at foot level and it is now also present for sound delivered at chest level, leading to an overturning of the localization toward the back . Finally, we tested whether the effect was specific to the dynamic audio stimulus used. To this aim, the verbal condition was replicated using a static sound. Again, there was an overall higher frequency of ‘back’ answers [(OR) = 0.18 ± 0.01, z.ratio = 13, P < 0.001], showing that there was significant overturning of the localization toward the back, at both elevation (Figure 3.6).

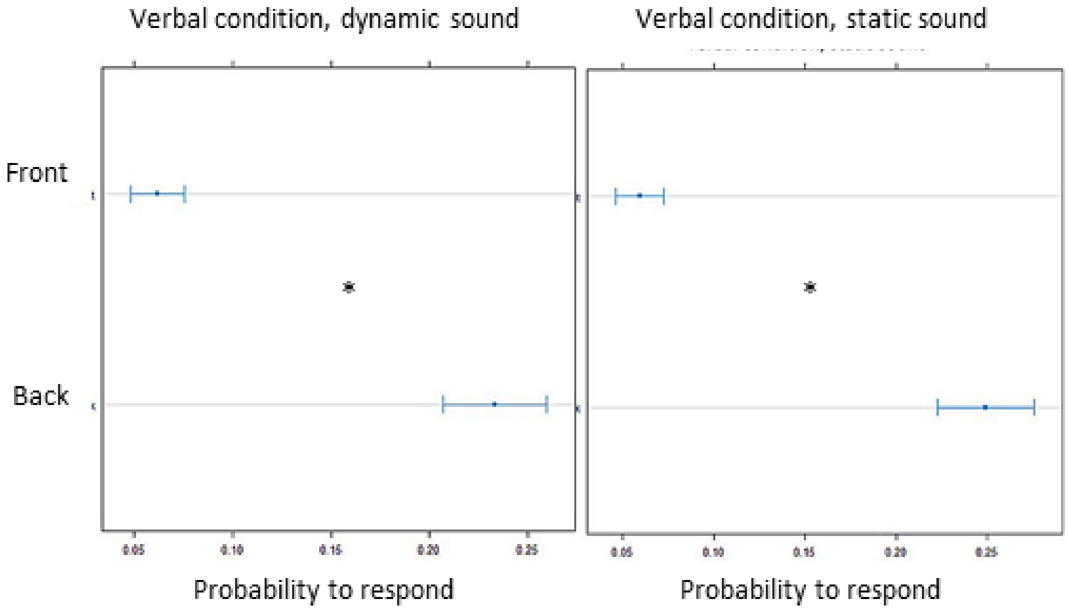

Figure 3.6 Proportion of verbal answers in the verbal pointing task with static (left) and dynamic (right)sounds: the plot represents the number of front and back answers given, independently of sound level. As can be seen greater number of ‘back’ responses were reported. Significant differences are illustrated ($*$ $P < 0.05$).

3.1.3 Conclusions of the experiment

Summarizing, our data showed a tendency to report frontal sound as coming from the back. This could be due to a shift toward the back or to a front to back error. Front to back errors explain the data found at foot level and in the oral task, while only a shift toward the back is present at chest level, when a motor pointing is required, suggesting that movement helps in discriminating front from back. We speculate that our brain build a representation of the space based on the reliability of sensory stimuli in those spaces. This could explain the greater number of front to back errors, suggesting that, when stimuli are not visible and auditory information is useless, back space becomes more salient, because there hearing is the only sense available to detect stimuli. This pattern could be due to adaptive mechanisms.

3.2 Exp2: Blindness, The Role of Visual Experience on Audio Space Perception around the Legs

It is unknown if the role of vision is similarly important in all portions of the frontal space. In this work, we investigated auditory perception and the role of prior visual experience in the space around the legs, by testing sighted and blind people. Auditory sound localization for front-back discriminations was measured in spaces where it is naturally possible to see (frontal space) and where it is not (back space), considering the body region between the waist and the foot. This task is particularly difficult, as ambiguity in binaural timing (interaural time difference, ITD) and level (interaural level difference, ILD) information often causes front-back confusions in sound localization. In order to understand the role of visual sensory experience in auditory perception in these spaces, auditory spatial localization was measured in sighted and, for the first time, in blind participants. Previous evidence (Schicke, Bauer and Röder, 2009; Aggius-Vella et al., 2017a, 2017b) suggests that the senses can differently influence or shape sensory information delivered in different areas of space. Previous studies have shown that blindness results in enhanced auditory localization performance for areas other than frontal relative to the participant, such as for azimuth judgements in peripheral space(Lessard et al., 1998; Teder-Sälejärvi et al., 1999; Voss et al., 2004). For this reason we hypothesised that blind people should perform better in a front-back discrimination task in back space compared to the front (Voss et al., 2008), where audition is the principal sense available.

3.2.1 Method

Eighteen participants were tested, N = 10 blind subjects (5 females, mean age and standard deviation 44 ± 19 years old, height: 163 ± 9 cm, see (3.1) and N = 8 blindfolded sighted subjects (4 females, mean age and standard deviation 31± 5 years old, height 165 ± 9cm). A between-subjects t-test confirmed that the groups of blind and sighted subjects were age matched, $t_{(16)} = 1.904$, $p = 0.08$. Participants were recruited on the basis of similar duration and level of school education (high school degree), normal hearing (assessed by an audiometric test), they reported themselves to have no cognitive impairments and to be right handed. The participants provided written informed consent in accordance with the Declaration of Helsinki, and the study was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy).

SUBJECTS	PATHOLOGY	AGE COMPLETE BLINDNESS	RESIDUAL VISION AT TEST	BLINDNESS DURATION (yrs)
Subj. 1	Retinopathy of Prematurity	Before birth	No vision	50
Subj. 2	Congenital glaucoma	Before birth	No vision	57
Subj. 3	Retinopathy of Prematurity	Before birth	No vision	29
Subj. 4	Corneal opacity	At 17yrs, visual performance decreased	No vision	11
Subj. 5	Retinitis pigmentosa	10 years of age	Lights and shadows	
Subj. 6	Leber's amaurosis	At 46 years of age	No vision	5
Subj. 7	Retinopathy of Prematurity	Before birth	No vision	51
Subj. 8	Maculopathy	Residual vision started at 69 yr	Residual vision	
Subj. 9	Uveitis	Before birth	Lights and shadows	27

Table 3.1 The table shows the age at test, the gender, the pathology (self-reported by the participants and based on a certification of blindness provided by a medical doctor), the visual status of each participant and the blindness duration (length of blindness).

The experiment was performed in a dimly lit room. As shown in (Figure 4.5, the apparatus consisted of 14 speakers split into two identical arrays of 7 speakers each (red and blue squares), vertically oriented. The lower speaker of each array was positioned at 4 cm from the floor, the others were situated at 19, 34, 49, 63, 78 cm and the highest was at 85 cm (as represented in Fig. 1), leading to 7 equivalent speaker vertical positions (i.e. 7 in the frontal space, and 7 in the back space). The two arrays were positioned facing each other. One array of speakers was placed in the frontal space (red array), slightly to the left (at 40° in relation to the face) and the other one in the back space (blue array), slightly to the left (at 160° in relation to the face). This configuration was adopted to reduce front-back error but maintaining task difficulty. The different angle size with respect to the midline (40° in the frontal space and –20° in the back space) made the frontal and rearward ITD and ILD values slightly different, helping the participant to discriminate between frontal and rearward sounds. Both arrays were situated at a distance of 50 cm from the position of the participant. During each trial, pink noise lasting 1 second was randomly delivered from one of the 14 speakers. Each speaker delivered the sound in six trials, for a total of 84 trials (42 trials in the frontal space and 42 in the back space). In order to clarify the representation of low space, for the analysis, we split the 7 equivalent speakers into two areas: 1) space above the knee (speaker numbers 4, 5, 6, 7, above 34 cm), and 2) space below the knee (speakers 1, 2, 3, under 34 cm). We decided to have the maximum height at knee level following previous work (Aggius-Vella et al., 2017a), as this is the main joint in the leg; it divides the leg into two separate segments, allowing free movement. Moreover, the two separate segments are involved in different ways in walking and receiving different sensory feedback. The area below the knee is mostly represented by tactile/proprioceptive and auditory feedback produced by walking, while the area above the knee drives leg movement and receives proprioceptive feedback, but it does not produce any sound. However, in the frontal space around the upper part of the legs, hands are frequently used and their movement is guided by vision, thus vision is likely the predominant sense in this space

All participants were blindfolded, led into the experimental room, and they then remained standing for the entire session. They were asked to keep their head straight and not to direct it toward the sound. They were instructed to verbally report whether sounds were delivered in the frontal or in the back area, without considering their elevations. Subject position and posture was continuously monitored and, if necessary, corrected by the experimenter. Sounds were administered by a custom made code in Matlab (R2013a, The Math Works, USA). The new trial started after the subject's answer, without any time restriction. The task took approximately 45 minutes.

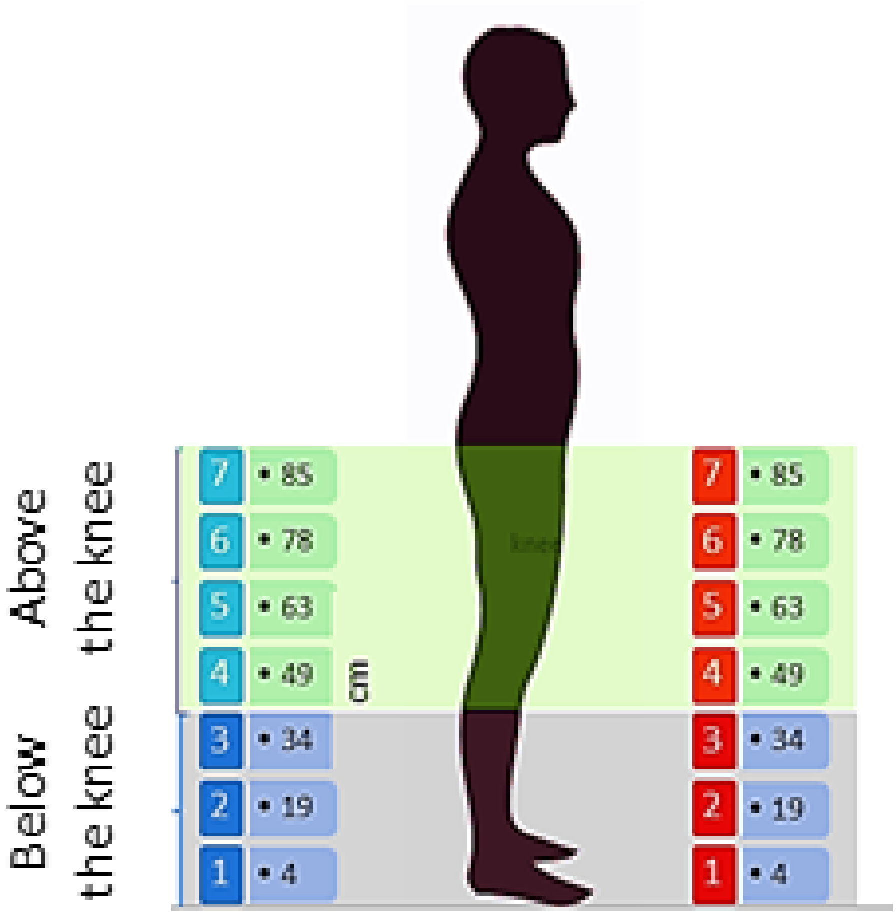

Figure 3.7 14 speakers were split into two arrays of 7 speakers each, vertically oriented. Speakers of each array were positioned at 4, 19, 34, 49, 63, 78 and 85 cm from the floor, leading to 7 equivalent speakers vertical positions in the frontal and back space. The two arrays were positioned facing each other.

Localization data were post-processed and analysed by a custom made program in R(R Core Team, 2016). The seven sound sources were grouped into two spatial levels: space below the knee (speaker numbers 1, 2, and 3) and above the knee (speaker numbers 4, 5, 6, 7). In order to evaluate the relation between sound localization and the role of senses in representing spaces, we analysed the pool of single trials using generalized linear mixed models (GLMM). In this way, we could estimate the variability of fixed and random effects (Moscatelli, Mezzetti and Lacquaniti, 2012). As our independent variable was binomial (1, 0), we applied GLMM with a logit link function and a binomial distribution. The benefit of using the GLMM is that the model takes into account the intrinsic binomial nature of the response variable, and overcomes issues with ANOVA related to departures from normality for analysing percentage data. With this analysis, two models were fitted for all subjects, taking into account the individual variability in the responses. We fitted the models to the choices from the localization task using the lme4 package (Bates et al., 2015) in the R statistical language (R Core Team, 2016). In the first model we took into account the correct answer; we regressed, in each trial, the answers of each subject (1=correct, 0= incorrect), as a function of speaker vertical position (above the knee vs below the knee) and longitudinal position (front vs back space) as factors within subjects, while considering group (blind vs sighted) as a between-subjects factor. While, in the second model (same dataset) we considered the perceived location of the sound (1=frontal, 0= back), as a function of speaker vertical position (above the knee vs below the knee) and longitudinal position (front vs back space) as factors within-subjects, while group (blind vs sighted) as factor between-subjects. These factors are included in our model as fixed effects, while subject as random effects. We calculated Analysis of Deviance Tables (using Type II Wald Chi-Square tests) for the models using the car package (Fox and Weisberg, 2011). For significant effects, we performed post hoc comparisons using the lsmeans package (Lenth, 2016), which computes and contrasts least-squares means (predicted marginal means). We adopted MVT P adjustment, which uses a multivariate t distribution. Contrasts, with P< 0.05 were considered as significant (corrected P values are reported). Only significant results are reported.

3.2.2 Results

Analysis of correct answers Analysis of deviance on correct answer showed a main effect of group ($X^2_{(1)} = 6.88$, P <0.001): sighted participants were significantly more accurate than blind (OR) = 0.62 +/-0. 11, z ratio = -2.53, P = 0.01. We found also a main effect of speaker vertical position (above the knee vs below the knee) ($X^2_{(1)} = 5.33$, P= 0.02): performances were better above than below the knee ((OR) = 1.3+/- 0.15, z ratio= 2.45, P=0.01). As well, we found a main effect of longitudinal position ($X^2_{(1)}$ = 5.05, P = 0.02): accuracy was higher in the back than in the frontal space ((OR) = 0.67+/-0.07, z ratio = -3.4, P < 0.001). (Figure 3.8) shows the interaction between longitudinal position and group ($X^2_{(1)}$= 4.26, P =0.03). Comparing longitudinal spaces within groups, blind subjects (on the left) reported a significantly lower probability (0.45 vs 0.6) to correctly locate sounds delivered in the frontal (red) than in the back space (blue), (OR) = 0.54 +/- 0.083, z ratio = - 3.9, P< 0.001). Instead, sighted participants (on the right) showed no difference in localizing sounds presented in frontal (red) and back (blue) space ((OR)= 0.84 +/- 0.14, z ratio= -0.96, P = 0.3). Comparing groups within longitudinal spaces, in the frontal space (see red points of Figure 2), blind people (on the left) performed worse than sighted people (on the right), showing a lower probability (0.45 vs 0.62) to correctly locate sound delivered in the frontal space (OR) = 0.50 +/- 0.10, z ratio= -3.18, P = 0.001. In the back space (see blue points of (Figure 3.8) no significant difference between the blind group (rhombus) and sighted group (circle) was observed, (OR) = 0.78 +/- 0.16, z ratio= -1.11, P = 0.3.

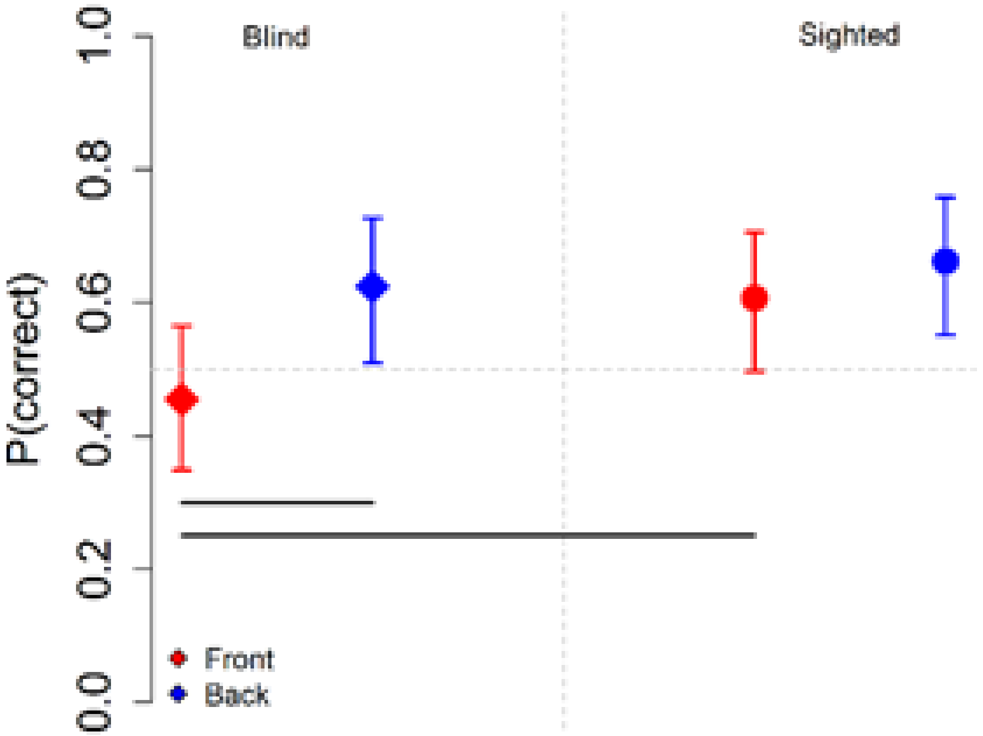

Figure 3.8 Interaction between group and longitudinal plane. Blind subjects reported a significantly higher probability to correctly locate sounds delivered in the back space than in the frontal space, while sighted subjects showed no significant differences in localizing sounds presented in frontal and back space. In the frontal space, sighted people performed better than blind people, while no significant differences between groups were found in the back space (bars represent significant differences).

(Figure 3.9) shows the interaction between longitudinal position and speaker vertical position ($X^2_{(1)} = 73.33$, P<0.001). In space below the knee (on the left), probability to correctly locate sounds was lower when the sound was delivered in the front (red arrow) than in the back space (blue arrow), ((OR) = 0.25+/-0.44, z ratio = -7.86, P<0.001). Instead, in space above the knee (on the right), the opposite pattern was found ((OR) = 1.81 +/-0.26, z ratio = 4.01, P<0.001).

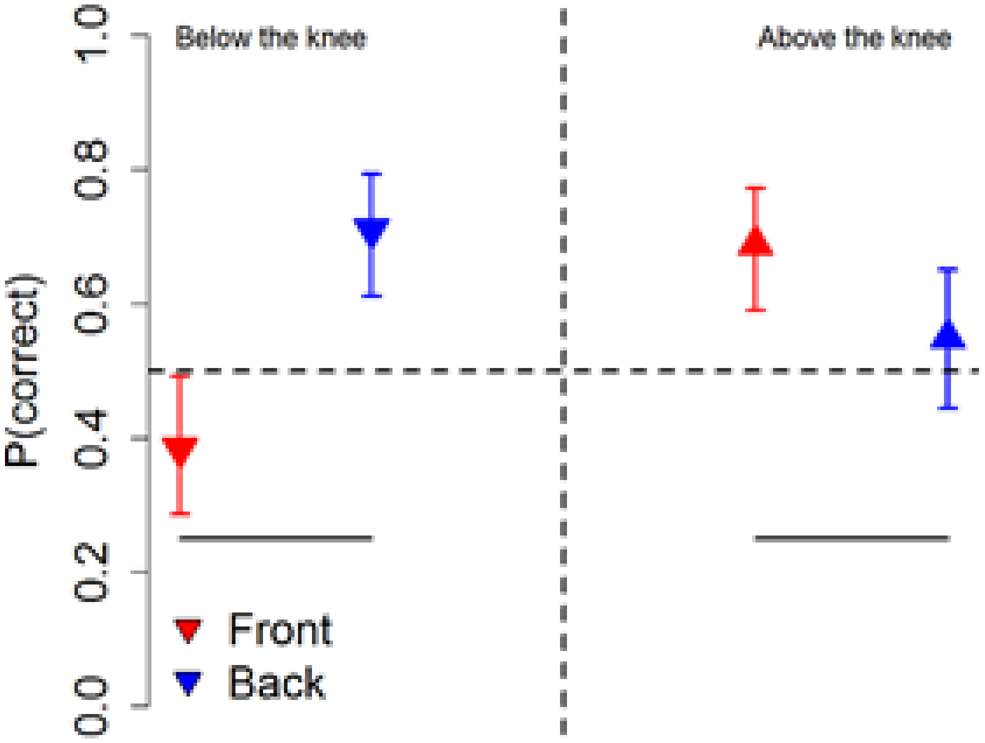

Figure 3.9 Interaction between speaker vertical position and longitudinal plane. As can be seen, subjects were more accurate in the back space (blue arrow) when sounds were delivered below the knee (left panel), while above the knee (right panel) subjects performed better in the frontal space (red arrow).

In summary, the results show that in frontal space, the sighted group localized sounds significantly more accurately than the blind group. In back space, no significant differences were observed between the sighted and blind groups. Moreover, our results reported a better localization in the frontal space, compared to the back, for sounds delivered above the knee, while a better localization in the back when sounds where delivered below the knee. This pattern of results is true for both groups.

Analysis of the probability on perception (i.e. of reporting a sound in frontal space). To be sure that the previous results were not due to perceptive bias (i.e. perceptual bias that could lead to give always the same response, leading to high accuracy in one space and low accuracy in the other), we performed an analysis taking into account the probability to report a sound in frontal space. Analysis of deviance on perceived sounds showed that the presence of vision did not produce any bias. Importantly, no significant differences between groups ($X^2_{(1)}$= 0.007, P = 0.93), between groups and longitudinal dimension ($X^2_{(1)}$= 0.005, P = 0.9), groups and elevation ($X^2_{(1)}$) = 0.18, P = 0.66) and between groups, longitudinal position and speaker vertical position ($X^2_{(1)}$= 2.2, P = 0.13) were observed. The differences found between groups on the analysis of correct answer seem not to be due to perceptual bias created by vision as in the present analysis, any factors interacted with groups, indicating similar perception in both groups. Indeed, we found a main effect of longitudinal position ($X^2_{(1)}$= 35.98, P<0.001): subjects showed a higher probability to report a sound in the frontal than in the back space ((OR) = 1.88+/- 0.21, z ratio= 5.56, P<0.001). As well, we found a main effect of speaker vertical position ($X^2_{(1)}$ =72.08, P<0.001): probability to perceive sounds as coming from the frontal space was higher above the knee (0.58 vs 0.34) ((OR) = 2.65+/- 0.30, z ratio= 8.53, P<0.001). An interaction emerged between longitudinal position and speaker vertical position ($X^2_{(1)}$= 5.17, P=0.02): probability to respond “front” was higher for sounds delivered above the knee in both spaces but the difference was stronger in the frontal space ((OR) = 3, 49 +/-0.56, z ratio = 7.73, P<0.001) than in the back space ((OR) = 2.01 +/-0.32, z ratio = 4.35, P<0.001).

In summary, an analysis of the probability of perception (i.e. of reporting a sound as originating in frontal space) showed that vision did not produce a bias toward frontal space. The results suggest that the differences in correct response between groups shown in the analysis in the previous section were not due to a bias (i.e. a tendency to give always the same answer).

Finally, we investigated whether the different history of blindness of participants within the blind group may have affected their performance. We applied GLMM with a logit link function and a binomial distribution. With this analysis, a model was fitted for blind participants, taking into account the individual variability of their responses. We regressed, in each trial, the answers of each subject (1=correct/front, 0= incorrect/back), as a function of speaker vertical position (above the knee vs below the knee) and longitudinal position (front vs back space), and residual vision (present vs not present), as factors within subjects. We did not find any significant effect which could suggest an influence of residual vision on results. In the second analysis, we applied GLMM with a logit link function and a binomial distribution. With this analysis, a model was fitted for all participants, taking into account the individual variability, blindness onset (age of complete blindness) and blindness duration (length of blindness) in the responses. We regressed, in each trial, the answers of each subject (1=correct/front, 0= incorrect/back), as a function of speaker vertical position (above the knee vs below the knee), longitudinal position (front vs back space), and group (blind vs sighted). The model of correct responses showed that later the onset of blindness, the greater the proportion of correct responses given in the frontal space only (p= 0.03), suggesting that during development vision calibrated hearing in the frontal space. Blind participants with a longer duration of blindness were more correct in the frontal space (p=0.02), and reported more sounds in the front (P= 0.0008), suggesting that movement (as we move and act mostly in the frontal space) may have a role in spatial representation. Blindness onset and blindness duration did not affect performance on speaker vertical position.

3.2.3 Conclusions of the experiment

In conclusion, our findings support the idea that vision plays an important role in developing an accurate perception of the location of auditory stimuli in the frontal space, and this influence is more evident in spaces far from the foot plane (going toward the head). Moreover, our data suggest a principal role for sound in the back space around the feet. Indeed, both group performed better in the back space, specifically at feet level. We think this effect is related to attention and/or sensory integration rules (when walking we received tactile and audio feedback on the foot, while vision is always forward to our feet, this can produce a lack of visual calibration in the front, while movement may 13 calibrate audition in back space). Further studies are needed to clarify this point. The current study shows for the first time that blind individuals are more accurate at performing front-back discriminations for sounds originating in back space compared to frontal space around the legs, whereas sighted individuals showed no differences in localization performance between sound presented from the front or the back. Measurements showed that both groups displayed higher localization performance above the knee than below for frontal sounds, and lower localization performance above the knee for sounds presented from the back. These results show that visual information plays an important role in calibrating hearing in frontal space. Furthermore, the results support and extend previous work demonstrating that auditory space can be divided into different regions above and below the knee49.

3.3 Exp3: The influence of time

As we have seen, there are many factors that influence special perception. One of these is time. The connection between time and space is well studied, it seems that both dimension are processed by a common system. If so, it is possible that, when vision cannot calibrate hearing, people rely on time to infer space. This was found in a recent study on blind people. In absence of vision, auditory spatial skills can be impaired when compared to sighted. In the following study, sighted and blind performed a bisection task with the time interval, between the 2 sounds, coherent or opposite to the spatial interval. The researchers found that the deficit disappears if congenitally blind individuals are presented with coherent temporal and spatial cues. We replicate the same study in front and back space, where vision is not available.

3.3.1 Method

A group of 6 sighted participants (mean age yo; F=) took part in the study. All participants reported no history of neurological or cognitive deficits. The research protocol was approved by the ethics committee of the local health service (Comitato Etico, ASL3 Genovese, Italy) and conducted in line with the Declaration of Helsinki. Written informed consent was obtained prior to testing. Stimuli and procedure Participants were sitting blindfolded in front of the center of an array of 23 speakers placed at a distance of 180 cm and spanning ±25° of visual angle (with 0° representing the central speaker, negative values on the left, and positive values on the right; (Figure 3.10). They performed two spatial bisection and one pure time bisection tasks, both in the frontal and rear spaces, leading to 6 conditions. The order of spatial blocks was randomized across subjects. In each task, subjects listened to a sequence of three consecutive sounds (500 Hz, 75 ms duration, 60 dB Sound Pressure Level (SPL)) for a trial duration of 1500ms. In spatial bisection tasks, participants judged verbally whether the second sound (S2) was spatially closer to first sound (S1;-25°, 0ms) or to third sound (S3; +25° , 1500ms). S2 could occur randomly at an intermediate position from -25° to +25°

in space, determined by the QUEST adaptive algorithm (Watson e Pelli, 1983). In order to evaluate the role of temporal cues in space performance, temporal intervals between the three sounds were manipulated to originate two different spatial bisection tasks (Figure 3.10): coherent time and opposite time spatial bisection tasks, with time intervals which could be coherent or opposite with respect to space distances respectively. In the coherent time spatial bisection task, spatial distances between S1-S2 and S2- S3 were directly proportional to temporal intervals between the three sounds (e.g. a shorter spatial distance between S1-S2 was associated with a shorter temporal delay between the two sounds). Considering that the total trial duration was 1500ms and the number of speakers was 23, when S2 was for example delivered from the second speaker on the left it was associated with a delay of 65ms, when it was delivered from the third speaker on the left with a delay of 130ms (65+65ms), and so on. In this condition, temporal cues could be used by subjects to infer spatial metric. Instead, space distances between the three sounds were inversely proportional to temporal intervals in the opposite time spatial bisection task (e.g. a shorter spatial distance between S1- S2 was associated with a longer temporal delay between the two sounds), making time informative but in the opposite direction with respect to space.

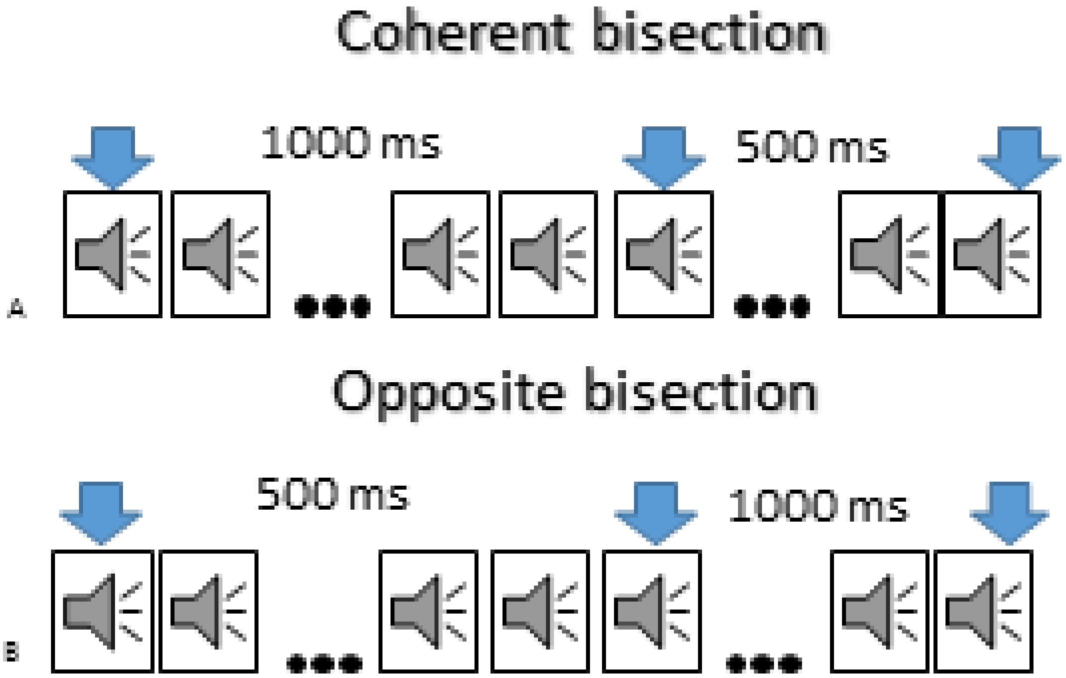

Figure 3.10 (A) Coherent spatial bisection: spatial distances and temporal intervals between the three sounds were directly proportional (e.g., long spatial distance and long temporal interval). (B) Opposite spatial bisection: spatial distances and temporal intervals between the three sounds were inversely proportional (e.g., long spatial distance and short temporal interval).

3.3.2 Results

Results showed that the variable time influences spatial representation of the back space, where vision is not present. A paired t test comparing spaces (front vs back) within the 2 conditions (coherent vs opposite) showed, in the opposite condition, better performance in the frontal compared to the back space ($t_{(5)}$ =-2.7, p=0.04), while no difference between spaces were found within the coherent condition ($t_{(5)}$=-1.3, p=0.1). Important, a t test comparing spaces within temporal bisection task, revealed that time is not better represented in the back space, compared to the frontal space ($t_{(5)}$=-7,3, p=0.5). This means that time interferes with space domain differently in the front and back spaces.

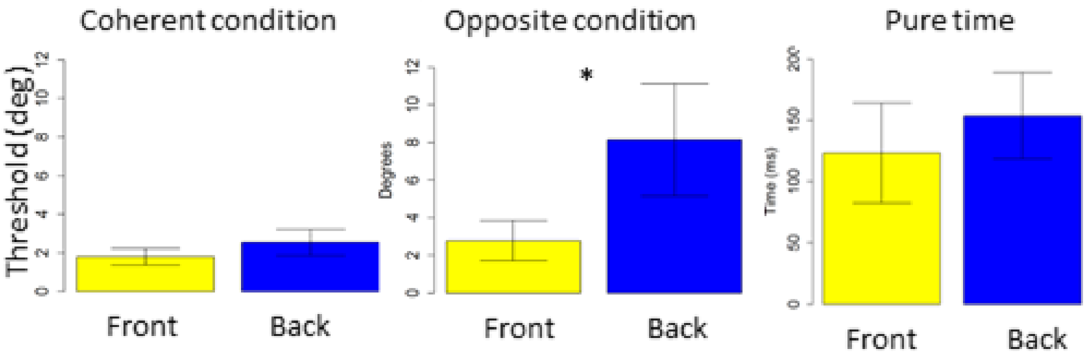

Figure 3.11 Yellow bars represent frontal space, blue bars represent back space. As can be seen, in the coherent condition (left) time helps in representing space leading representation to the back space similar to that in the frontal space, while in the opposite condition, time decrease spatial representation in the back space but not in the frontal, where vision calibrated hearing(center). Interesting no difference in time representation are present between the 2 spaces(ledt).

3.3.3 Conclusions of the experiment

It seems that, where vision is present, a solid spatial representation is built, so reducing the bias produced by the time1. Instead, in the back space, where the lack of vision does not permit to calibrate hearing, the representation of space is more affected by interference produced by time1, (Figure 3.11) .

3.4 Interim conclusions

As we have seen, discriminate front from back sound is quite difficult, due to the cone of confusion. From all our experiments, it seems that people tend to report sounds delivered in the frontal space as coming from the back space (exp 1 and 2) This discrepancy between spaces could be attributed to the fact that vision is unavailable in the back. The lack of the principal sense could make hearing more salient in this space so, when our brain is uncertain on where the sound come from, it tends to locate it in the back space. However, this effect can be modify by movement; indeed, in the first experiment it has been shown that movement influences the audio–visual representation of high frontal space, suggesting that the increased accuracy, found in the motor condition for sounds delivered at chest level, is not related to a mere perceptual effect. As the improvement in localizing frontal sounds seems to be specific for the upper part of the body, in experiment 2 we focused our attention on space around legs. Indeed this space is still less investigated despite its importance in task as walking. It is possible that vision has a different weight in this space, as it is not always linked with sound produced by footstep (we usually not look our feet while walking). In this experiment, blind and sighted people performed a front back discrimination task. Results suggest that the absence of vision produces an improvement in some portions of space, where vision is not present. Finally, if hearing is more important in the back space and if hearing is the principal sense for time perception, we hypothesized in the back space people follow time instead space.

Chapter 4

The role of vision and audio-motor feedback on spatial perception

Blindness is a condition that offers the possibility to study the influence of vision on the development of auditory spatial perception. The lack of vision leads to changes in the perception and elaboration of sounds at a neural level Elbert et al. (2002); Stevens and Weaver (2009). For example, early blind individuals showed more efficient processing of auditory stimuliGougoux et al. (2004), by reporting an expansion in areas responsive to auditory stimuli and a decrement in signal response latenciesElbert et al. (2002). However, the nature of these modifications is still unclear. A review Thinus-Blanc and Gaunet (1997) shows contrasting results on the relation between lack of vision and spatial representation. While some studies have shown enhancements in some aspects of spatial representation, others have reported an impairment in some features of spatial hearing. For example, it has been shown that blind individuals have improved skills such as horizontal sound localization Doucet et al. (2005); King and Parsons (1999); Lessard et al. (1998); Lewald (2007); Röder et al. (2004)and relative distance discriminationKolarik et al. (2013); Voss et al. (2004a). On the other hand, other works have shown that some spatial skills are impaired in the absence of visual input, as shown in early-blind humans during several tasks as: the localization of end point of a dynamic soundFinocchietti et al. (2015), the audio space bisection (Gori et al., 2014), the evaluation of the absolute distance Kolarik et al. (2013), the auditory spatial representations of the extrapersonal space in both: reverberant and anechoic environments, for speech, music and noise signals Kolarik et al. (2017) and the vertical localization of a sound source Zwiers et al. (2001). The reason why some auditory spatial skills are enhanced and other impaired in blind individuals is still an open question. Similarly, the effect of sensory loss on cortical activity is still matter of debate. Some studies reported that when the most appropriate sense for a specific ability is lacking, such as vision in spatial cognition, the silent pre-existing connection is revealed and leads to new strong connections Amedi and Meijer (2005); Dahmen and King (2007). This thesis is supported by several imaging studies Eckert et al. (2008); Frasnelli et al. (2011); Gougoux et al. (2005). However, other imaging studies provided an evidence for reduced connectivity between visual and auditory systems, as well as between visual and somatosensory systemsBurton et al. (2014); Liu et al. (2007); Yu et al. (2012), supporting instead the idea that these heightened abilities reflect re-programming of visual cortex for "metamodal" purposeBurton et al. (2014). As well as vision, also body movements have an important role in spatial cognition. This idea is supported by the motor-oriented approach, which assumes that spatial relationships are coded by body movement in the space Paillard (1991). Our brain represents space based on the possibility to directly act on it (within/outside hand-reaching distance). Moreover, our actions can change the representation of space, in peripersonal space for example, the training with a tool modifies the extension of the body space, that in turn affects spatial representation, making what was previously far away seem closer Berti and Frassinetti (2000). Motor and auditory system are strictly related in the brain, neuroimaging studies have shown that simply listening to an auditory rhythm engages motor areas in the brain Grahn and Brett (2007). This sensory-motor integration is at the base of actions execution. During development, children use visual information to construct a sense of space by associating visual and motor related signals. The success of an action is monitored by matching the expected change of sensory, mostly visual information, with the observed changes. These sensory-motor feedback loops are principally important in early infancy and childhood. Recent studies suggest that the communication between sensory modalities is fundamental for a correct unisensory and multisensory development. For example, the visual information seems to be fundamental for the development of spatial perception in the haptic modality Gori (2015); Gori et al. (2008, 2010, 2014, 2011); Vercillo et al. (2016) and inaccurate visual signals can provide clear effects on the development of correct spatial information in the auditory system Knudsen and Knudsen (1985). Brambring, showed that the development of spatial capabilities is also driven by the reciprocal influence between visual perception and execution of movements. It is important to note that sensory-motor learning is not sensory-modality-specific, but that a novel sensory-motor information can be transferred between sensory modalities Levy-Tzedek et al. (2012). Based on these evidences, it is possible that a natural or a specific audio motor training improves auditory spatial representation by substituting the visual feedback with the auditory feedback. Recently, our group developed a new rehabilitative technology for blind and low vision people called ABBI, the Audio Bracelet for Blind Interaction. The idea behind ABBI is that it is possible to rehabilitate the spatial and social deficits by exploiting a natural audio-motor association. ABBI can be positioned in different part of the body. It produces an audio signal that provides spatial sensory feedback of the body in the space (it is similar to the visual feedback used by sighted children). Indeed, the audio movement will convey spatial information, that, in turn, are used to build spatial representations in an intuitive and direct manner. In this chapter will be presented two experiments showing the importance of audio motor feedback in recalibrating spatial perception. The first study show as natural training involving audio motor integration, as playing football, can completely restore spatial representation, leading blind people to perform as sighted people. In the second experiment, instead, it will be shown as a specific training, with ABBI device, can improve spatial perception around feet also in sighted people.

4.1 Exp1: The role of vision andsport training on audio spatial representation.

Blind football is played according to the traditional football rules of the Fédération Internationale de Football Association (FIFA) with adaptations that enable blind people to participate. To help players' orient themselves, the ball is equipped with a noisemaking device that allows players to locate it by sound, and verbal communication within the team makes the players aware of the locations of their colleagues and opponents. The role of football players is to locate the ball in the space and intercept it. Moreover, the components of the team should rely on auditory information to build a dynamic representation of the football field's configuration. It is possible to see this sport as a natural training linking auditory and motor feedback. We have already seen that this multisensory integration could enhance perceptual and spatial cognitive abilities. The development of training methods on the basis of scientific evidence and assessments aimed at improving performance may potentially be exported outside the sport frame to help all the visually impaired people. In this experiment, I will show how the natural audio motor feedback, played by football players, is able to restore spatial representation in these athletes compared to normal blind.

4.1.1 Method

Thirty-six subjects took part in the experiment, and all participants confirmed they had normal hearing and no cognitive impairments. Three groups were formed on the base of subject's characteristics. The first group was composed by twenty-one sighted subjects

(7females and 14 males) aged 28±11years (mean±SD). The second group was composed by eleven blind subjects (5 females and 6 males) aged 30±9 years(mean±SD). The last group was composed by four blind professional football player (4 males) aged 29±4 years (mean±SD). All subjects performed the spatial bisection task and the minimum audible angle in a randomized order. Subjects were blindfolded before entering a normal experimental room (echoic), so they had no notion of the room or the speaker layout. Subjects were standing at a distance of 80 cm from the stimuli and aligned with the center of a bank of 11 speakers, spanning respectively ±23.6° of visual angle, at ear level, distance between 2 near speakers was 7cm. The position was continuously monitored by the experimenter. We used an onset abrupt pink noise lasting 100ms, for which both interaural time differences and interaural level differences are important; the sound was well heard from every subjects. For the spatial bisection task, three 100ms stimuli were presented successively at 500ms intervals between 11 speakers, the first at -23.6° (at ear level), the third at +23.6° (at ear level), based on condition, and the second at an intermediate speaker (between the first and third sound, 9 possible speakers) position determined by the QUEST adaptive algorithm52, which estimates the point of subjective equality after each response, and places the next trial near that estimate. Subjects reported verbally whether the second sound was closer to the first or to the last sound. Each subject performed 60 trials for each condition. For the minimal audible angle task, two 100ms stimuli of 500Hz were presented successively with a 500ms interval, one (randomly first or second) on the central speaker (0°), the other at a certain distance left or right, following the QUEST algorithm. Each task was carried out in two different positions (front and back), resulting in two randomized conditions: frontal ear, back ear. In order to perform the task in allocentric coordinates, the spatial order of the three sounds was always the same, independent from the position of the subjects. This means that, in the frontal condition of the bisection task, the first sounds started from the left of the subjects' position, while in the back condition the sound started from the right (same absolute position in the space but different in relation to the body). In the MAA, in the frontal conditions the subjects reported which of the two sounds was located further right, and in the back conditions, which was further left (see (Figure 4.1)). Each subject performed 60 trials for each condition. For the spatial bisection task, the proportion of "third" responses was calculated for each speaker distance, while for the MAA task the proportion of right or left (in accordance with condition) was calculated. 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) and conducted in line with the Declaration of Helsinki.

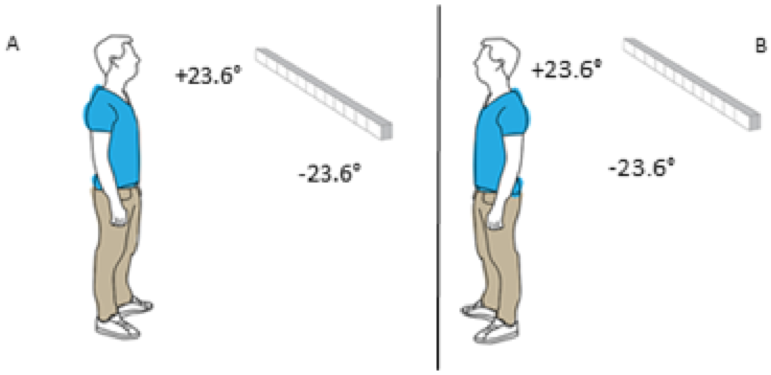

Figure 4.1 Set up and tasks. The spatial bisection task was performed at ear in both frontal (A) and rear (B) space. Three sounds were delivered from the three different speakers. Subjects had to judge whether the second sound was closer to the first or to the last sound. The spatial order of the three sounds was fixed in the space (they always started from the same speaker). Minimum audible angle task: the task was performed at ear in both frontal and rear space. Subjects had to judge the position of two sounds. In the frontal condition, subjects had to report which of the two sounds was further right, while in the rear condition, they had to state which of the two sounds was further left. Temporal bisection was performed at ear in both frontal and rear space. Three sounds were delivered from the same speaker with different delays between each other, and subjects had to judge which was the shortest interval between sounds.

4.1.2 Results

Three groups of subjects, for a total of thirty six people, participated in the experiment and performed a total of 3 tasks, namely spatial bisection, minimum audible angle (MAA) and temporal bisection. Each task was carried out in two different positions (front and back (Figure 4.2)). For each task, each condition (i.e. position) consisted of 60 trials, for a total of 360 trials for each subject. For each condition, a psychometric function was calculated. For each subject and condition, the space constant *sigma* of the fit was taken as the estimate of threshold for all tasks. Space constants were converted from centimeters to angles. We conducted 2 different analysis. In a first analysis, we conducted a permutation Anova separately for the front and back position to reduce the complexity of the model, given the relatively low statistical power due to the low number of player participants. We used the aovp function of the lmperm R package. We performed post-hoc comparisons using permutation t test, using the perm.t.test function of theDeducerRpackage.We considered $P<0.05$ as significant, after applying holm correction for multiple comparisons (mean and standard error are reported). Anova performed on the frontal bisection task with factor group (sighted, blind and blind football player) (Fig. 2 right) showed a difference between groups ($F_{((2,44)}$ =3.8, p=0.02). Blind football players reported higher precision (lower threshold) (t=-2.22, P=0.02) than blind. As well, sighted subjects reported higher precision (lower threshold) (t=-1.5,P=0.04) than blind. Finally, no differences were reported between blind football players and sighted (t=2.48, P=1). The same analysis was performed on the MAA and showed no differences between group ($F_{(2,44)}$=2.74, P=0.07).

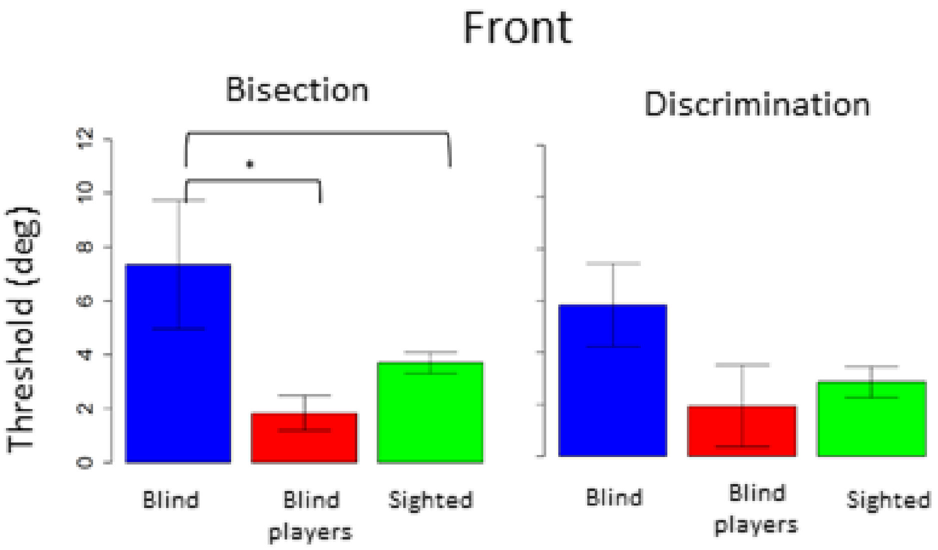

Figure 4.2 In the frontal space (left) Blind football players (red bars) performed like sighted (green bars) and like echolocator Vercillo et al. (2015) and better than blind (blue bars). No differences betwee groups where found in the MAA (right). Error bars represent standard errors.

Both analyses on bisection and MAA tasks were performed on the back (Figure 4.3). Anova showed a difference between groups ($F_{(2)}$ =3.65, p=0.03). Blind football players reported similar precision (t= -2.2,P>0.05) than blind. As well, sighted subjects reported significant higher precision (lower threshold) (t=-2.1, P=0.02) than blind. Finally, no differences were reported between blind football players and sighted (t=0.61,p>0.05). Analysis performed on the MAA showed no differences between group ($F_{(2)}$ =2.74, P=0.07), (Fig.3).

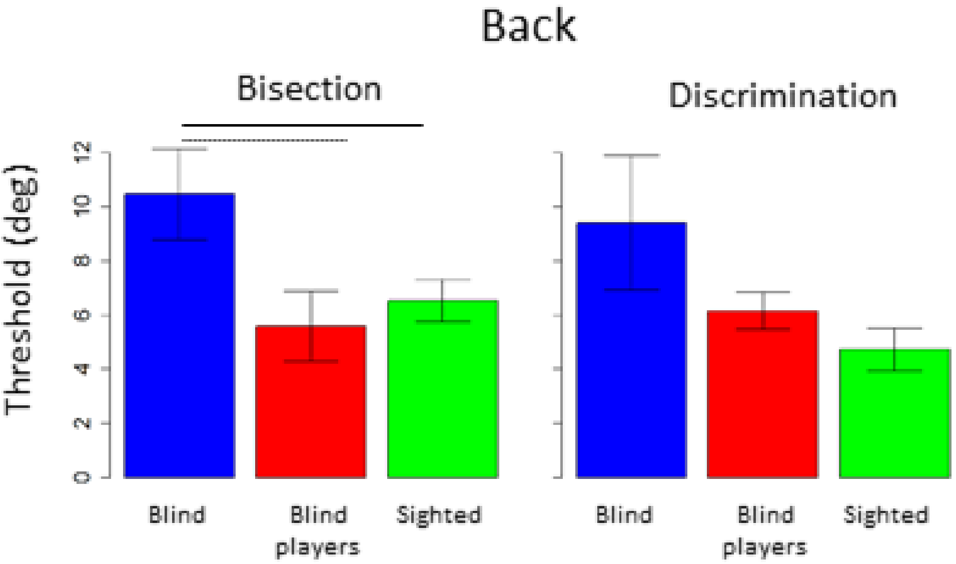

Figure 4.3 In bisection task (left), in the back space, Blind football players (red) performed like sighted (green), while blind subjects (blue) performed much worse. No differences between groups in the MAA (right)

We have not done an Anova with factors space (front vs back) and group (blind, blind football players and sighted), as statistical power would have been not enough. However, we were interested in investigating front back spatial representation inside the groups. With this purpose, we performed t test between spaces inside each group. Sighted group showed better performance in the frontal space compared to the back (t= -3.21, p<0.01). Blind group performed similarly in the 2 spaces (t=-1-06, p=0.31). Blind football players group performed better in the frontal space (t=-2.59, p=0.79, uncorrected p=0.039). By the way, as show in figure 2 and 3, this group performed better than the others in both spaces No differences in all groups were found in the MAA, see (Figure 4.4).

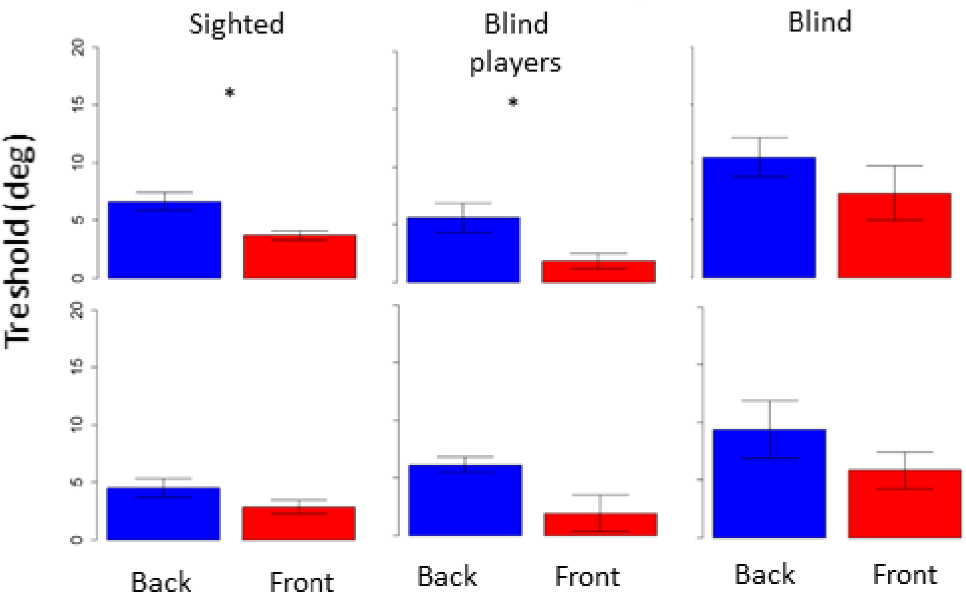

Figure 4.4 Front (red) back (blue) thresholds are similar in blind football players (center) and sighted (left). No differences between front and back in blind group (right)

4.1.3 Conclusions of the experiment

Summarizing we have seen that blind football players perform spatial bisection in the frontal space as sighted. Moreover, they seem to show better performance in front and back spaces compared to the other 2 groups

4.2 Exp2: The role of audio motor training in improving spatial representation

This paragraph presents another kind of rehabilitation program, always based on audio motor feedback. The concept of using sounds and movements to improve spatial representation is the same of the previous experiment, but in this case we use a rehabilitative device ABBI that can be used on all kind of subjects (also very young child as old people). Previous works from our group mainly focused on the recalibration of spatial representations around the upper body portion of space in blind individuals Finocchietti et al. (2017), no studies have investigated whether the use of this device can be also useful to improve spatial representations around the lower body part in sighted individuals. Improvement of space representation at the lower body part would be important for the rehabilitation of locomotion and legs mobility functions in individuals with motor disabilities. With the aim of improving space representation around the lower body portion in sighted individuals, here we studied their audio space representation before and after a training with ABBI positioned on the subject's foot. In order to investigate an improvement of audio spatial precision, we used a front-back sound discrimination task. As already seen, this task is really difficult also for sighted people, as involves spaces where front back error are frequents. Forty five sighted subjects, split into three groups, performed two sessions (before and after a training) of an audio localization task, in which they had to judge if a sound was delivered in the frontal or back space. The experimental group performed 2 min of audio motor training with ABBI between the two audio tests, while no audio motor training was performed by the control groups, where subjects completed just 2 min of free leg movement without sound, or 2 minutes of passive sound's hearing.

4.2.1 Methods

Forty five participants were enrolled in the study. Subjects were randomly split into three age ($F_{((2,42)}$ =0.13, P= 0.87) and height ($F_{((2,42)}$ = 1.35, P = 0.37) matched groups: experimental group, which did the audio motor training (N = 15; 11 females, age: 26 ± 5, years old, height: 165 ± 9) cm; motor control group, which did only motor training (N = 15; 5 females, age: 27 ± 6 years old, height: 170±2) cm and audio control group, which did only audio training (N = 15; 7 females, age 26 ± 3 years old, height:170 ± 1) cm. All the participants had a similar educational background, no cognitive impairments, were right handed, and they reported to haven't any hearing impairment (we administer an online hearing test to be sure all participants had the same hearing perception). 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).

Set-Up and Sound Localization Task The experiment was performed in the center of the same dark reverberant room. All participants were positioned in the middle of the room, far from each wall, so that reverberant noise was the same across subjects. As shown in Figure 1, the apparatus consisted of 14 speakers split into two arrays of seven speakers each, vertically oriented; the lowest speaker of each array was positioned at 4 cm from the floor, while the others were situated at: 19 cm, 34 cm, 49 cm, 63 cm, 78 cm, the highest being at 85 cm. There were therefore seven equivalent sound elevations in the frontal and rear space. The two arrays were positioned facing each other; one array of speakers was placed in the frontal space (at 40° in relation to the face) and the other one in the rear space (at 160° in relation to the face); both arrays were situated at a distance of 50 cm from the subject's position. During each trial, pink noise lasting 1 s was randomly delivered from one of the 14 speakers. Each speaker delivered the sound in six trials, for a total of 84 trials for each session (42 trials in the frontal space and 42 in the rear space). As our goal was to clarify the representation of auditory space around the legs, we split the seven equivalent speakers into two areas: above the knee space and below the knee space, as shown in Figure 1. Above the knee space referred to speakers (numbers 5, 6 and 7-up to 34 cm), while below the knee space (speaker number 4) was represented by (speakers 1, 2 and 3-under 34 cm). We decided to use the knee because it divides the leg into two separate segments, allowing free movement. The knee is also involved in walking and leg actions, and so could influence spatial representation of the two leg segments. Participants were blindfolded and led into the experimental room, where they remained standing for the entire session (they were allowed to rest before the training). They were asked to keep their head straight and not to direct it toward the sound. They had to verbally report if sounds were delivered in the frontal or in the back area, without considering their spatial elevations. Subject position and posture were continuously monitored and corrected when necessary by the experimenter. Sounds were administered by a custom-made code in Matlab (R2013a, The Math Works, USA); the experimenter recorded on text the oral answer given by the subject ("Front" or "Back") for the consequent analysis. The entire experiment was performed at the participant's own pace and each trial started after the subject's answer, without any time constraints.

Protocol The auditory localization task, as previously described, was performed in two sessions (about 20 min each), spaced out by 2 min of training (Figure 4.5). The experimental group underwent audio-motor training with the sound source (digital metronome with single pulse 500 Hz, intermittent sound at 180 bpm), delivered by ABBI, placed on the left ankle; they were asked to move their left leg and consequently the sound, from the frontal position to the rear and vice versa, to freely explore space around the body. It was required a continuous and constant movement. The short timing for the audio-motor training was chosen because a previous study (Finocchietti et al., 2017) showed that the spatial recalibration is fast, thanks to the association of the auditory feedback with a voluntary movement. Two control conditions were performed. One control group (motor control group) performed only the same free leg movement, by repeatedly moving the leg from the front position to the back position (as in the group trained with ABBI) but without audio feedback associated to the movement. The second control group (audio control group) listened to the ABBI sound moved by the experimenter with known position. In this case, the experimenter provided before the sound in front and afterwards in the back (random order) by communicating to the subject the spatial position of the sound: the sound was presented for 1 min in the front and for 1 min in the back. The subjects of this group received the same amount of sound feedback as the experimental group. After the training, all groups performed the second session of the sound localization task.

Data Analysis Localization data were post-processed and analyzed by a custom made program in R (R Development Core Team, New Zealand). We removed speaker number 4 (49 cm) from the analysis, as it was at the edge between space below and above the knee level. The six sound sources remained were grouped into two spatial levels: below the knee (speaker numbers 1, 2 and 3) and above the knee (speaker numbers 5, 6 and 7), t test confirmed no differences inside these two spatial portions. In order to evaluate the relation between sound localization and the role of senses in representing spaces, we analyzed the pool of single trials using generalized linear mixed models (GLMMs). In this way, we could estimate the variability of fixed and random effects. We applied GLMM with a logit link function and a binomial distribution. Our model was random-slope (or maximal) following Barr guidelines Barr et al. (2013)and was set for all subjects, taking into account the individual variability in the responses. We set the model to the choices from the localization task using the lme4 package Bates et al. (2015) in the R statistical language. The model took into account the correct response; to do this, we regressed, in each trial, the answers of each subject considered the correct answer (1 = correct, 0 = incorrect), as a function of sound level (above the knee vs. below the knee), longitudinal position (front vs. back space) and session (pre vs. post) as factors within subjects, while group (experimental vs. motor control and vs. audio control) as factor between subjects. These factors are included in our model as fixed effects. We calculated Analysis of Deviance Tables (using Type II Wald chi-square tests) for the models using the analysis of variance (ANOVA) function of the car package. For significant effects, we performed post hoc comparisons using lsmeans package, which computes and contrasts least-squares means (predicted marginal means). We adopted Holm P adjustment. Contrasts with $P < 0.05$ were considered as significant (P corrected are reported). Data are presented as mean ± standard error.

4.2.2 Results

Results on the analysis of deviance showed a multiple interaction between longitudinal space (front vs. back), sound level (above the knee vs. below the knee), session (pre vs. post) and groups (experimental, motor and audio control) $X^2_{(2)} = 11.86$, $P = 0.002$. (Figure 4.6) shows

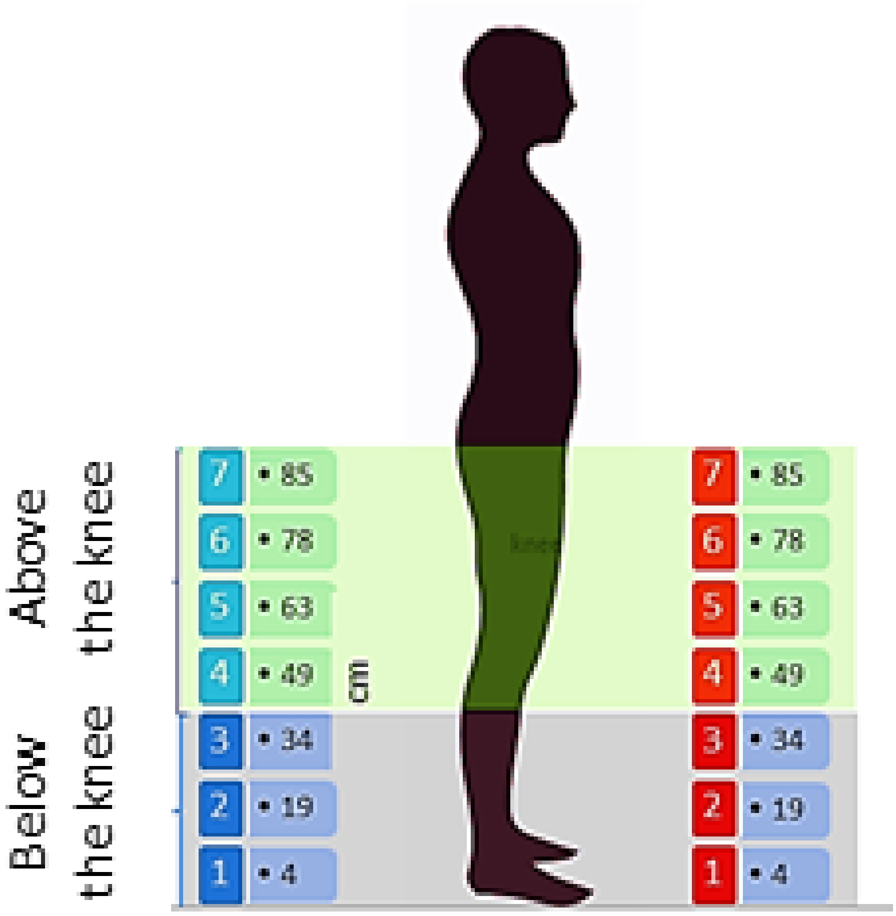

Figure 4.5 14 speakers split into two arrays of seven speakers each, vertically oriented; speakers of each array were positioned at 4 cm, 19 cm, 34 cm, 49 cm, 63 cm, 78 cm and 85 cm from the floor, creating seven equivalent sound elevations in the frontal and rear space. The two arrays were positioned facing each other, one in the frontal space and the other in the rear space.

this interaction in terms of performance's variations, i.e., the difference (post session-pre session) of the probability to respond correct calculated by the lsmens function for the post hoc contrasts based on the GLMM model. Green bars represent sounds delivered above the knee level, red bars represent sounds delivered below the knee level; light colors denote sounds delivered in the frontal space, while dark colors denote sounds delivered in the back space. Positive values of the bars represent improvement in performance in the post session compared to the pre session, and negative values represent decrement in performance. As can be seen, only the experimental group showed performance's variations after the training. Specifically, considering the back area, an improvement is present in space above the knee (dark green bar; (OR) =1.7 ± 0.36, z.ratio = 2.9, P = 0.01) and below the knee (dark red bar; (OR) = 1.91 ± 0.4, z.ratio = 2.8, P = 0.01). Instead, in the frontal space, an improvement is visible above the knee (light green bar; (OR) = 2.04 ± 0.5, z.ratio = 2.5, P = 0.02), while a performance worsened below the knee (light red; (OR) = 0.48 ± 0.09, z.ratio = 3.8, P = 0.0006). Therefore, performance's variations in the frontal but not in the back space were strongly dependent on the elevation at which sounds were delivered.

A second interaction was found between longitudinal position, session and groups $X^2_{(2)} = 10.90$, P = 0.004. (Figure 4.7) explains this interaction in terms of performance's variations. Blue bars represent back space, while red bars frontal space. As can be seen, an improvement is present only in the experimental group and only in the back space ((OR) = 1.85 ± 0.2, z.ratio = 3.94, P = 0.0005).

Moreover, a third interaction was found between sound level, session and groups $X^2_{(2)} = 8.02$, P = 0.01. (Figure 4.8) describes this interaction in terms of performance's variations. Red bars represent sounds delivered above the knee and green bars sounds delivered below the knee. An improvement is present only in the experimental group and only for stimuli presented above the knee ((OR) = 1.91 ± 0.32, z.ratio = 3.77, P = 0.0009).

4.2.3 Conclusions of the experiment

To conclude, we showed that an audio motor training below the knee modifies the representation of space around the leg, probably by impacting on different multisensory integration processes. This could explain the improvement and decrement in performance in different zones around the legs. Future experiments should be performed to explore the brain plasticity of the recalibration mediated by the use of ABBI and its application in people with motor disability.

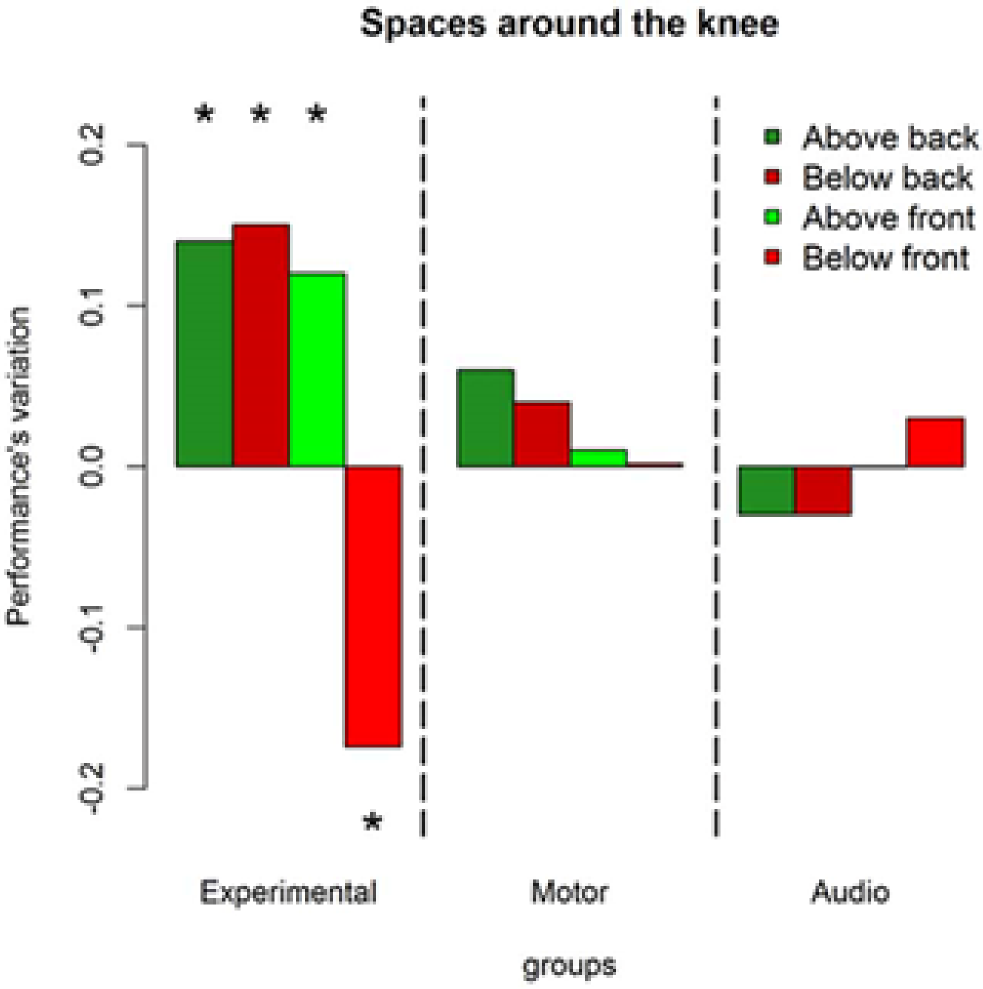

Figure 4.6 . Performance's variation in each space after the training. Green bars represent space above the knee, red bars denote space above the knee. Dark colors are used for the back space, while light colors are used for the frontal area. As can be seen only the experimental group shows performance's variations (post—pre) after the training, leading to an improvement in the back space and to a worsened performance in the frontal space under the knee. ∗Indicates P $<$ 0.05.

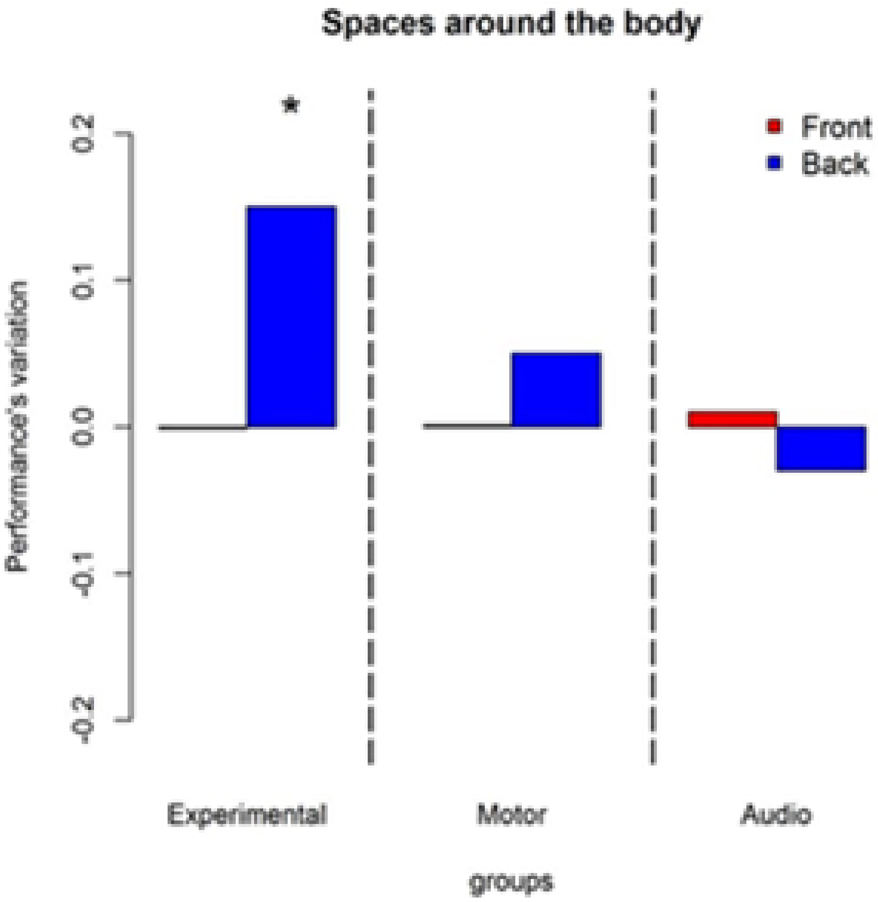

Figure 4.7 Influences of training on longitudinal position: represent performance's variation (post—pre) in discriminating front-back location without considering body elevation. Red bars denote frontal sounds, blue bars represent back sounds. As can be seen only the experimental group improved. The improvement is present only in the back space. ∗Indicates $P < 0.05$.

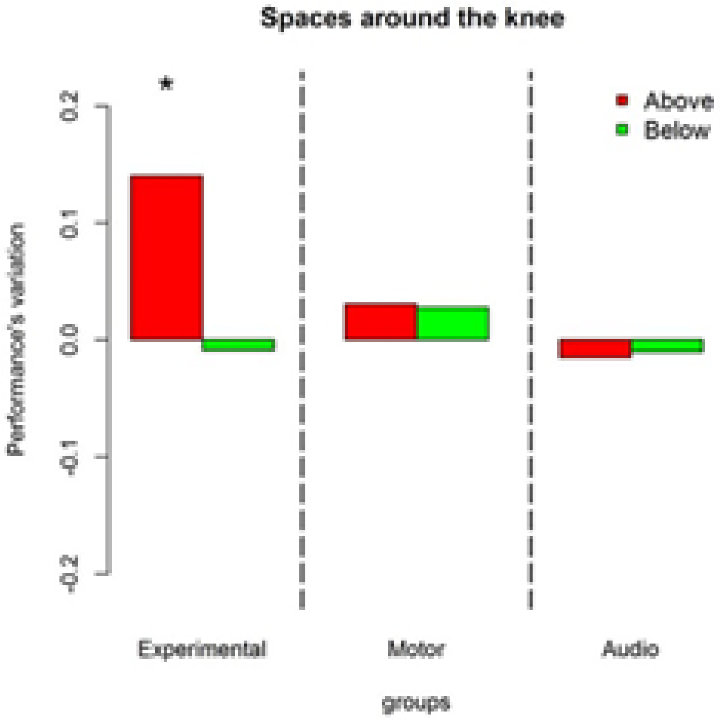

Figure 4.8 Influences of training on longitudinal position: represent performance's variation (post—pre) in discriminating front-back location without considering body elevation. Red bars denote frontal sounds, blue bars represent back sounds. As can be seen only the experimental group improved. The improvement is present only in the back space. ∗Indicates P < 0.05.

4.3 Interim conclusions

These two experiments supported results presented in chapter 1 and 2 by showing again that front and back space are different represented and that this difference is mainly due to the presence of vision, as blind people perform similarly in the two spaces. Moreover, the innovation of these 2 studies regard the possibility to improve and also restore spatial representation trough specific audio motor training. Indeed, the rehabilitative effect seems to be due to the sensorimotor association that facilitates multisensory integration. Previous studies have shown that audio-motor associations are easily encoded by our brain and transferred across senses Levy-Tzedek et al. (2012). The flow of information between auditory and motor cortex seems to be bidirectional, and arbitrary sounds (without a previous motor or verbal meaning) can be rapidly mapped onto the motor system Ticini et al. (2012)). These results suggest that, despite the exercise is natural as sport or specific, as the training with ABBI, the link of sound and movement actives neural connection useful for representing space.

Chapter 5

General discussion

It is known that attentional processes split the space around the body in several portions differently treated by the brain. However, senses are spread out among the body in a fixed way, making the sensory modalities differently available across spaces(i.e. vision in the front, hearing everywhere). Several findings suggest that each sensory modality and the body movement are at the base of cognitive skills. However, it is still unknown if this sensory organization contributes to the different representation of spatial portions and, more in general, to the different developing of cognitive skills in each space.
The aim of this work is to investigate if and how sensory modalities and body movement of different effectors influence the coding and the representation of spaces around our body.

We tested auditory spatial representation of sighted individuals in space where the visual information is naturally availabe (e.g. front space) and where it is not (e.g. back space), the same tasks were administred to a group of blind individuals, for which the same difference should not be evident. Finally, we tested audio-motor integration could improve spatial representation in space where vision is not present. In this way, we were able to test how vision, hearing and movement affect the representation of spaces around the body. Our thesis is that the different sensory coding of spaces could lead to develop different skills among spaces, like spatial representation. As we have seen in the introduction, space is not coded by our brain as a unitary dimension, but, instead, is split up in multiple subspaces differently analysed by the brain. This differentiation between spaces is based on attentional resources, as shown in neglect patients. In this work, we have shown that portions of spaces around the body are also different on cognitive skills developed on the base of the sensory modality available, we may speculate that the spaces are not different only for attentional mechanisms but also for perceptual process.

Role of vision among spaces It is known that, during the first years of life, sensory modalities communicate with each other and become calibrated through interaction with physical reality Gori (2015). This process is fundamental for the development of unisensory and multisensory skills. Gori et al. (2008) showed that in a visual-haptic integration task, children (younger than 8 years of age) show unisensory dominance rather than bimodal integration and the modality that dominates is task specific: the haptic modality dominates size perception and the visual modality dominates orientation perception. In other words, this dominance could reflect a process of cross-sensory calibration, where in the developing brain the most robust modality is used to calibrate the others Gori (2015); Gori et al. (2011). A good deal of evidence suggests that the calibration process may be fundamental to acquire specific perceptual concepts: in particular Gori et al. (2012, 2010) have shown that the impairment of the system that should calibrate the other impacts on the modality that needs calibration Gori et al. (2012, 2010, 2011).However, body structure makes spaces around the body different for the kind of sensory modality available. This is a crucial point because sensory modalities have different roles in developing cognitive skills. Specifically, we tested the role of vision on spatial representation skill in different portions of space. Our results suggest that the presence of vision produces a difference between front and back spaces. Sighted people, indeed, performed better the spatial bisection task in the frontal space than in the back, while blind people performed similarly in the two spaces (exp2 chapter 3) and perform worse in the frontal space compared sighted (exp2 chapter 3 andGori et al. (2014)). We can conclude that spatial representations of frontal and rear spaces are different due to the presence of vision. If this result could be inferred by previous results on blind, the novelty of these studies is that the visual dominance on spatial perception is specific for the spaces were vision is present and it does not affect spatial representation of other spaces. The results presented in this thesis leads to suggest that, in the back space, sighted people are like blind people in terms of spatial representation. Besides the difference in the quality of spatial representation, spaces around the body could be different on the base they are built. Bisection task has usually been assumed to be performed most efficiently using an allocentric reference frame, as this allows direct assessment of the positions of different sound sources (as opposed to referring the position of each source to the head/body and then inferring the spatial separation of the sources). MAA, instead, has been assumed to require a spatial judgment that might be more anchored to an egocentric frame of reference rather than an external frame of reference. Comparing these 2 tasks across spaces, we found that the representations of these spaces are built by using different reference frame. The head could be a good reference to represent the space around it in egocentric way; while, the poorer representation of feet leads the space around them to be better represented by allocentric coordinates that do not involve body representation. Interesting also front back spaces differ on the base of the coohordinate used. Frontal space seems to be represented trought both allocentric and egocentric reference frame, while the back space is better represented by egocentric reference frame. This result could be explained by the fact that vision is necessary to develop allocentric frame of reference, while egocentric frame of reference do not need it, as also blind people are able to use it. More interesting, we found that people performed better bisection task than MAA in the lateral space, probably because the cues used for spatial bisection are not adversely affected by front-back confusions. Until now, we have spoken mostly about azimuthal dimension of spaces, however, each space has also a longitudinal dimension (judgment of the distance), that it is important in order to build a representation of the environment and guide locomotion. However, spatial representation in depth dimension is less studied and we don't know the tools our brain uses to represent this dimension. We found that reverberation causes difficulties with bisection judgements for clicks but not for speech and noise in sighted people. This suggests that different factors (i.e. kind of sound and room type) influence spatial depth representation. However, basing on our data it is difficult to say if vision calibrate hearing in distance dimension in the same way as azimuth bisection.

Role of hearing Hearing is the only sense that is available among every spaces. It can be use in the near, far, frontal and back spaces. It can also be used to detect stimuli hided to vision. Moreover, hearing differently from vision, cannot be turned off, it works also during sleeping. Hearing is not the best sense for spatial representation, but, due to its particular characteristics, it should be important in some skills. It was suggested, hearing is the dominant sense in temporal domain. This hypothesis is supported in previous work, where Gori et al. (2018) found that blind people use time information to represent space. and by results obtained in experiment 3 of chapter 2, where we were able to see the influence of time in representing frontal and rear space. Interesting, we found that time information affects mostly back spatial representation than the frontal one, suggesting that hearing has a predominant role in the back space that, in turn, leads the back space to be more influenced by temporal info compared to the frontal one. , If so, its role should be more visible in the back space, as in the frontal space, vision can detect easily the stimuli. Our results showed that around the chest and around the feet, subjects are generally more accurate in localizing sounds presented in the back space. On the contrary, in the frontal zone they are less accurate and reported a large number of front–back errors. As revealed by the analysis on bias, localization error was mainly due to longitudinal space (x-axis), showing a great bias toward the back on both elevation. Interesting in the verbal condition, front–back errors were present at both elevation. This data supports the role of movement in spatial perception. Indeed, movement can improve sound localization by reducing front back error and this is more evident in the space where we usually operate (i.e., high frontal space). To disambiguated if the auditory localization of frontal and rear auditory space was related to the body part considered or to the involvement of body movement, we asked to subjects to localize sounds trough a verbal answer. Indeed, if the front back error was due to the effector used or to movement in general, it should have disappeared in the verbal condition. This was not the case at foot level, where a great number of front to back errors were still present, suggesting that localization error at this level was due to different sensory representations of these two spaces. However, in the pointing motor task, the bias toward the back was present at both elevations, but only data at foot level were explained by front to back error, suggesting that motor command plays a significant role in discriminating front from back sounds. Crucially, in the verbal condition, front–back errors were also found at chest level. We think that the possibility to move significantly reduces error in localizing frontal sounds around the chest, probably because in this space we are used to integrating sensory feedbacks with actions Goodale (2011); so localizing sounds at this level could be seen as a sort of reaching Perris and Clifton (1988). These results cannot be explained by cone of confusion, as in all tasks the reversal error was unidirectional (from front to back). In general, we suggest that the greater localization error toward the back could be considered as an adaptive mechanisms due to the availability of different senses in that space. The visual modality, indeed, is crucial for space representation and stimuli detection, but it is not available in the back space; for this reason, auditory modality could be more salient there. In agreement with this idea, it has been shown that, when audio–visual stimuli are delivered frontally, vision dominates the final perception, weighting more in multisensory estimation Alais and Burr (2004). Importantly, this explanation is related to the simple localization task, while vision is necessary to develop a more refined spatial map, for example, that required in the spatial bisection task (Gori et al., 2014). It is known that movement affects spatial representation, however, few studies tested space around legs. We tested sighted and blind subjects in order to see the influence of vision in space above the knee, where hand movements or audiomotor information(Aggius-Vella et al., 2017a) may play a role in calibrating space and space below the knee, where auditory and/or tactile information from footsteps may play a role. This study was realized also to understand if, the different employment of vision in space around the upper part of the body and in space around the lower part of the body, could lead to different sensory integration rules. For example in space where hands usually operate, it is possible that spatial congruency is fundamental, as when we usually use hands, we perceive audio-visual and tactile feedback in the same place (i.e. on the hand). While, it is possible that, the spatial congruency fails in space around feet, as when we walk, we perceive sound and tactile feedback on the foot but we usually look forward. As expected, in space where vision is not present (i.e. the back), the two groups performed similarly, while the presence of vision allowed a better localization in the frontal space. Interesting, the fact that sighted people do not show difference between front and back, suggest that sound localization do not need of visual calibration. This explanation is also supported by the fact that blind people performed better than sighted in the back space. Crucially, this last data valorized again the attentional hypothesis. Indeed, if the back space is a space where hearing has a more efficient attentional role, and if, as found in literature, blind people are more sensible to sounds, it derives that blind people should perform better in the back space.

Role of multisensory integration as substitution of visual feedback. While in chapter 1 and 2, we focused on visual and hearing perception, in chapter 3, we investigated the role of audio motor integration in spatial cognition. To this end, we tested two different kinds of spatial training based on audio motor integration. In experiment 1 chapter 2, we showed as a "natural" audio-motor training (i.e. football for blind) could restore spatial representation leading blind people to perform as well as sighted people. In this experiment, we tested three groups of people: blind people, blind professional football players and sighted people, in spatial bisection and MAA tasks, in front and back paces. As expected, in the frontal space professional football player performed like sighted people, moreover both (sighted and blind football players) groups performed better than blind, while no differences between groups were found in the back and in spatial acuity (MAA) in frontal and back spaces. The same good spatial perception in blind people was found in a group of echolocatorsVercillo et al. (2015). These results suggested that spatial representation could be shaped and rehabilitated by different factors. Interesting, we found that also front back representation of football players is similar to that of sighted (i.e. better in the front compared to the back), while no difference between the 2 spaces were found in blind people. Basing on the rehabilitative power of audio motor integration in restoring spatial representation, in experiment 2 chapter 3, we tried to rehabilitate space around legs by using a rehabilitative device, called ABBI. This device produces a sound when it is moved. Placed on the body, it creates a link between body movement and sound produced by it. In this way movement guides (trough proprioception) hearing in the space by calibrating it. This is the same procedures, applied by vision, during hearing calibration. Several successful studies showed the efficacy of ABBI for frontal spaces in the upper part of the body Cappagli et al. (2017); Finocchietti et al. (2015); Giorgio Zini et al. (2017); Gori et al. (2016); however, it was still unknown if also representation of space around leg follows the same multisensory integration rules that are at the base of hearing calibration and, so, if the representation of this space could be restored by this kind of rehabilitation. Our study consisted in 2 phases of test (front back discrimination task) interposed by two minutes of experimental training (moving from front to back the leg dressing ABBI device), motor control training (move from front to back the leg, without producing any sound) and auditory control training (passively hearing a sound moving from front to back). As predicted, only the experimental group improved in the post training session. Crucially, the improvement was related to the back space, where vision is not present. This result is interesting because show as hearing is differently calibrates in frontal and back space: where vision is not available, movement contributes to develop spatial representation. Another interesting result came from this experiment is that audio-motor training affects differently high and low spatial body representation. This result can be explained by considering how often the auditory feedback is linked to those body parts. Indeed when walking, only body space around the foot is mapped by hearing, thanks to the audio feedback produced by the foot reaching the floor: this might be automatically linked to the tactile and proprioceptive information used to encode the leg spatial position. The training with the ABBI device might be less beneficial in the lower portion of the body because at the foot level, a natural audio-motor association is already present and it is mediated by locomotion. Another possible speculation is that different multisensory process acts above and below the knee. During locomotion we usually look in front of our feet so visual experience occurs independently respect to the audio-proprioceptive integration related to feet. Since experience can modulate audio-visual integration (Meredith and Stein, 1996), it is plausible that the audio information associated with walking is integrated with proprioceptive feedback on the same spatial area but with visual information congruent in time and not in space. Thus, a possible speculation is that this sensory misalignment could lead to distorted or less automatic sensory integration. The training with ABBI might reinforce this misaligned association. The same distortion is not present above the knee because in this body zone the audio feedback of movements is not present and multisensory integration is similar to the upper body part where the sensory-motor training with ABBI is useful for spatial recalibration Finocchietti et al. (2017).

Chapter 6

Conclusion

To conclude, with these works, we provided evidences that space around our body is not only split in multiple portion on attentional base but also on cognitive skills developed by different sensory modalities. More precisely, we showed that vision is dominant in spatial representation and its effect is evident only in the frontal space. Indeed sighted people show a difference between front and back space, when performing spatial task. The same difference is not present in blind people. Moreover, we showed that hearing is the more reliable sense for temporal task, its role seems to be predominant in the back space, as it is the only sense to detect stimuli in this space. Finally, we have seen that audio motor integration can improve spatial representation and could be used as training for spatial rehabilitation. All evidences fitted in the context of a theoretical framework proposing that the senses play different roles in cognition and their effects are differently shared among the various regions of space. In future works, we are going to investigate in deep the influence of hearing and movement in the various spaces. At the moment we are testing spatial perception in emiplegyc children to see if they present different spatial representation between the healthy and emiplegyc part of the body space. Morover, we are developing a new rehabilitative device for motor impaired people that has the goal to convert motor feedback in auditory feedback, allowing so, people without propioception to perceive their body moving in the space. Finally, we are investigating the neural correlates (EEG) underline representation of different spaces. All these findings have a dual goals to acquire new knowledge on the role of senses in cognition and to develop new rehabilitative devices based on scientific evidences. To know how our brain organizes and administers resources, among senses and spaces, adds knowledge on how our brain optimizes cognitive resources in time (we have limited cognitive resources to spend at the same time) and could be important for rehabilitative program.

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