

# SPACE IN LANGUAGE

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# SPACE REPRESENTATION IN THE ABSENCE OF SIGHT IN THE HUMAN BRAIN

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## 1. PREFACE

Despite the lack of vision, blind individuals are capable to move independently in space, to represent identity and to localize objects and relate with them, to catch other people's intentions and feelings, to develop a social communication. More than that, blind individuals very often make us notice some specific sensorial aspects that we are simply 'unable to see': a specific timbre of the voice that conveys information of one's feelings, a sudden mild change of temperature while walking around the corner, a peculiar scent in front of a grocery store, an unusual texture of a textile.

Since the early days, sight has always been regarded as the most important sense for humans to interact with the environment and to acquire knowledge. In the ancient Greek language the verb 'to know' (οἶδα) was the past tense of the verb 'to see' (ὄραω), that is, "*I saw and thus I know*". Similarly, everyday linguistic uses such as "*can you see my point?*" or "*I see what you mean*" suggest a predominant role of vision. Furthermore, from a neuro-anatomical perspective, almost one third of the whole cortex in primates is devoted to visual function.

These few considerations alone are enough to raise some fundamental questions. How do individuals with congenital blindness form a representation of a world that they have never seen? How is non-visual sensory information processed in the brain in sighted and congenitally blind individuals? What happens to the "visual" brain in congenitally blind individuals? To what extent is vision really necessary for the human brain to develop and function?

In the last two decades, behavioural and functional brain studies in individuals with congenital blindness have provided a powerful approach to understand how the external world is represented, and how the brain functional organization develops in the absence of sight.

In this chapter, we will discuss findings from studies conducted in sighted and congenitally blind humans relative to spatial abilities and representation.

## 2. IS VISION NECESSARY TO DEVELOP SPATIAL ABILITIES?

While for a long time vision has been thought to be crucial for the development of spatial abilities (e.g., Howard and Templeton 1966), a growing body of studies has begun to indicate that the lack of visual experience may have just minimal effects on spatial performance (e.g., Thinus-Blanc and Gaunet 1997).

The mental representation of several cognitive functions (including the domains of mathematics, music, language, or learning), are spatial in format (Hubbard *et al.* 2005; Beecham *et al.* 2009). Moreover, spatial localization and representation are necessary for motion discrimination, motor planning or action understanding (Johnson *et al.* 1996; Wise *et al.* 1997). Additionally, spatial abilities often relate to the individual ability to navigate in the surrounding space, a fundamental ability in everyday life. Altogether, these spatial-related abilities critically rely on mental imagery, the mental representation of the space itself, and thus on specific frames of reference.

### 2.1. *Mental imagery and spatial processing in sighted and blind individuals: similarities and differences*

Mental imagery is referred to as “a *quasi-perceptual* experience”, as mental imagery significantly resembles sensory/perceptual experience, but occurs in the absence of the appropriate perceptual stimuli (Eysenck *et al.* 1972).

In spite of the fact that imagery, often referred to also as “the mind’s eye”, is classically coupled to visual perception, several studies converge in showing similar performance levels in sighted and blind individuals in tasks typically assumed to require object or scene imagery (e.g., mental scanning, object perceptual categorization) (e.g., Paivio and Okowita 1971; Vecchi 1998; Tinti *et al.* 1999; Kerr 1983; Zimler and Keenan 1983). Additionally, when the familiarity of material is controlled for and the context is optimized (Heller *et al.* 1999; Bliss *et al.* 2004), blind people may be even able to form and manipulate mental images which rely on ‘visual’ features, such as shape, object-related words, and also colors for the late blind individuals – (Cornoldi *et al.* 1979; Marmor 1978).

Interestingly, blind people may not only show a comparable performance but also use mental processes similar to those used by sighted participants, as demonstrated by studies with a dual task paradigm (Vecchi 1998; Aleman *et al.* 2001; Fleming *et al.* 2006). For example, when required to mentally analyze the shape of different objects (main task), the impairment produced by a concurrent finger-tapping spatial task (parallel task) in congenitally blind was

similar to sighted individuals, thus suggesting that both groups were relying on similar mental strategies (Aleman *et al.* 2001). Despite the fact that mental images can be associated to visual or sensory-traces, and thus may share mechanisms common to distinct senses, perception and imagery are at least partially independent and do not necessarily require visual perceptual experience (e.g., Aleman *et al.* 2001; Vanlierde and Wanet-Defalque 2004).

In contrast, as compared to sighted controls, congenitally and late blind individuals may present different responses or encounter selective limitations in performing imagery tasks if visual experience or visually-based interfering effects are employed (e.g. “visual-impedance-effect” – Knauff and Johnson-Laird 2002, or verbally-induced illusions – Renier *et al.* 2006), or when involving complex spatial mental abilities, for example continuous updating or active manipulation of stimuli (Reiser *et al.* 1986; Vecchi 1998). As a matter of facts, congenitally blind individuals can count on a limited amount of sensorial information, in terms of both classical visual spatial features (such as perspective or angle representation) and their simultaneous and integrated perception. These perceptual limitations may be reflected on slower or impaired performances that occur mainly at a higher cognitive level, and suggest the possibility that congenitally blind individuals rely on partially different non-visual spatial processes (Arditi *et al.* 1988; Noordzij *et al.* 2007; Vanlierde and Wanet-Defalque 2004). For example, dealing with multiple or with three-dimensional mental representations is rather problematic for congenitally blind individuals (Cornoldi *et al.* 1991, 1993; Vecchi 1998; Vecchi *et al.* 1995, 2004), probably because their cognitive mechanisms have been developed on the basis of a sensorial perception mainly through touch and hearing, which only allow for a sequential processing of information (Cornoldi *et al.* 1998; Loomis *et al.* 1991) and may limit the combination of multiple items (Cattaneo *et al.* 2008).

Consistently, Thinus-Blanc and Gaunet (1997) hypothesised that the observed differences between sighted and visually-deprived individuals may be related to a lack of appropriate strategies: the *quantitative* advantages of vision (such as precision and amount of information available simultaneously) would lead to *qualitative* differences in encoding spatial information. Therefore, because the spontaneous organization of non-visual cues (auditory, kinaesthetic or haptic) is more temporal rather than spatial, even if blind individuals are capable of using parallel processing, they tend to form mental images with reduced information, as complex representations that require higher loads of computation are more difficult (see Vecchi *et al.* 2004, 2006).

On the other hand, blind individuals may balance the lack of vision both at a perceptual level, by enhancing their non-visual discrimination (Röder *et al.* 1999, 2000; Goldreich and Kanics 2006; Lessard *et al.* 1998), and at a higher cognitive level, by developing conceptual networks that depend on non-visual

inputs (Bull *et al.* 1983; Hull and Mason 1995; Röder and Neville 2003; Röder and Rösler 2003; Röder *et al.* 2001). Similarly, under specific circumstances, the higher expertise with non visual representation of objects may facilitate their processing of spatial features, such as tri-dimensionality or perspective (Ballesteros and Reales 2004; Eardley and Pring 2006; Revesz 1950; Kennedy and Juricevic 2006; Heller *et al.* 2005), thus suggesting that these notions may be part of blind people's mental imagery.

On line with these findings, research on spatial cognition (i.e., the ability to orient, move and interact with our environment) indicates that congenitally blind individuals can perform similarly to blindfolded sighted individuals in many navigational tasks (e.g., Morrongiello *et al.* 1995; Ungar *et al.* 1993, 1994; Dufour and Gérard 2000; Noordzij *et al.* 2006; Fortin *et al.* 2008). For example, Passini *et al.* (1990) showed no differences between congenitally blind and blindfolded sighted subjects when learning a new route in a labyrinth.

The permanent or temporary lack of visual input in blind or blindfolded sighted individuals, respectively, seems to promote the generation of route-like (sequential) instead of survey-like (simultaneous) representations of space (Vecchi *et al.* 2004; Tinti *et al.* 2006). Because of the simultaneous perception of the environment, vision enhances an 'organized' representation of the space as a whole (Millar 1981; Hausfeld *et al.* 1982) and facilitates the transformation in externally-defined (allocentric) frame of reference (Röder *et al.* 2004; see also Hötting *et al.* 2004), also during visuomotor control and planning. In contrast, blind individuals tend to rely on more egocentric and experience-based representations (Postma *et al.* 2006; Rossetti *et al.* 1996). For example, a crossed hand posture has detrimental effects in reaction times during temporal order judgments or localization tasks in sighted and late blind individuals, while this does not occur in early or congenitally blind individuals (Collignon *et al.* 2009; Röder *et al.* 2004, 2007).

On the other hand, Tinti *et al.* (2006) demonstrated that blind people may be even more efficient than blindfolded sighted persons in a series of survey-representation based tasks. Thus, blind people can also benefit of the survey-like perspective of a map, as they may be able to transform a series of two-dimensional relationships into a truly three-dimensional space. Indeed, the use of two-dimensional tactile maps considerably facilitates the performance of blind individuals, other than the simple direct experience of a layout by walking around (Ungar *et al.* 1993; Espinosa *et al.* 1998).

Nonetheless, the results of many spatial imagery and navigational task studies are still controversial, likely also because of the specific nature of the experimental paradigms and the heterogeneity of the populations recruited (see Cattaneo *et al.* 2008 for a review).

## 2.2. Cortical pathways for object and spatial visual perception and imagery

In the last three decades, the advent of in vivo brain functional exploration techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), have offered a unique tool to investigate perceptual, cognitive and affective brain functions in humans (Pietrini *et al.* 2003; Raichle 1998, 2003). In a task-related brain region, glucose and oxygen consumption, and blood flow increase in relation to local increases in neuronal synaptic activity. Brain functional methodologies are able to measure these physiological parameters that represent reliable indices of neuronal-synaptic activity across distinct cortical and subcortical structures in the brain (Raichle 1998, 2003). In addition, transcranial magnetic stimulation (TMS) recently has proven to be an useful method to interfere with neuronal function in specific brain regions and to assess the consequent effects on behavioral performance (Miniussi *et al.* 2010; Rossini *et al.* 2007).

Since the early '80s, brain functional studies have focused on the investigation of visual perception and representation, and of visual-based imagery processes. The advancing in experimental paradigm design together with the improvement in data acquisition and analysis – also due to the development of MR imaging at high and ultra-high fields that have increased greatly both temporal and spatial resolution (e.g. Yacoub *et al.* 2007; Hoffmann *et al.* 2009) – is making it possible to obtain a more and more defined structural and functional characterization of the neural correlates, not only of visual perception in early visual region cortex, but also of higher-order processing and recognition of visual stimuli in extrastriate cortical areas (e.g., Haxby *et al.* 2001; Kriegeskorte *et al.* 2009).

The initial brain functional studies have shown that also in humans the extrastriate visual cortical areas are organized in two anatomically and functionally distinct pathways, in a fashion similar to that revealed by single neuron recording in non-human primates (Ungerleider and Haxby 1994; Haxby *et al.* 1994). The “ventral stream”, also called the “what” pathway, projects to the inferior temporal cortex and forward to the frontal pole, and is mainly activated during visual object recognition. Specifically, this part of the cortex is capable of producing highly specific patterns of neural response to distinct categories of objects (Haxby *et al.* 2001). The “dorsal stream”, also known as the “where” pathway, projects to the posterior parietal areas, and is involved in spatial localization, motion processing, and action planning (Haxby *et al.* 1991, 1994). These brain networks, that process complementary and integrated aspects of visual perception, subserve also visual imagery processes in sighted subjects (Kosslyn *et al.* 1999a, 1999b; Ishai *et al.* 2000, 2010).

As a more general principle, the “*quasi-perceptual*” experience of imagery (visual or non-visual, such as tactile, auditory, gustative or olfactory) shares common neural substrates with the related specific sensory perception, supporting the hypothesis of a direct top-down control on primary sensory and multimodal brain areas during imagery (Ishai *et al.* 2010).

### 2.3. *Beyond vision: supramodal functional cortical organization in the human brain. From object representation...*

To what extent is this specific functional organization in the ventral and dorsal visual pathway cortical areas preserved in individuals with congenital loss of sight? In other words, in which measure is visual experience a mandatory pre-requisite for the brain to develop this functional organization?

Several recent experimental pieces of evidence support the hypothesis of the existence of *supramodal* cortical regions in the human brain, that is, brain areas able to process information regardless of the sensory modality through which such an information has been acquired. Although congenital blindness usually determines a functional reorganization of the early visual regions – that are recruited to process information delivered through other sensorial channels, including tactile, auditory, smell or gustatory stimuli (Amedi *et al.* 2005; Cattaneo *et al.* 2008; Cuevas *et al.* 2009) – blind people as well as sighted individuals rely on supramodal brain areas in order to perform and process perceptual and imagery tasks (Cattaneo *et al.* 2008). That is, supramodally organized cortical areas are physiologically present in the human brain and are not the results of plastic reorganization that also occurs as a consequence of sensory deprivation (Pietrini *et al.* 2004, 2009).

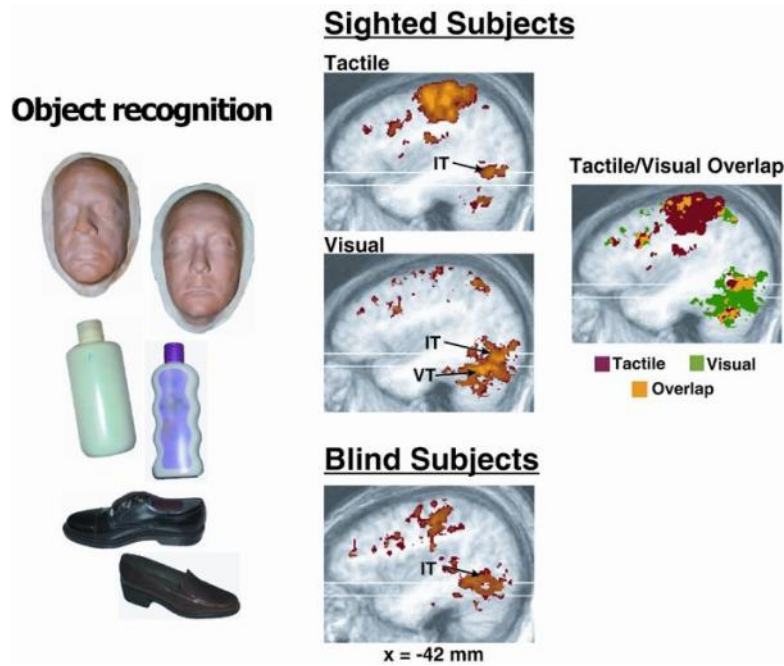


Figure 1. Brain areas that responded during visual and/or tactile object perception in sighted and congenitally blind individuals. Sagittal images from group Z-score maps of activated areas are shown. The inferior temporal (IT) and ventral temporal (VT) regions activated by visual and/or tactile perception of the three object categories shown above are indicated. The tactile/visual overlap map shows the areas activated by both tactile and visual perception (shown in yellow), as well as the areas activated only by tactile (red) and visual (green) perception in the sighted subjects (modified from Pietrini *et al.* 2004)

In a pioneer study, the category-selective recruitment of inferior temporal and ventral temporal extrastriate visual cortical areas found in response to visual stimuli (Haxby *et al.* 2001) was demonstrated also during tactile recognition of different object categories in blind-folded sighted individuals, supporting the hypothesis that these regions may provide a *supramodal* representation of objects, and may thus be involved in the processing of information of object form regardless of the sensory modality through which the information is acquired (Pietrini *et al.* 2004; see Figure 1). Moreover, these category-selective responses were reported also in congenitally blind individuals during tactile recognition of distinct object categories, thus indicating that the development of topographically organized, category-related representations in the extrastriate “visual” cortex does not require visual experience to develop nor is it dependent on a visual-based imagery (Pietrini *et al.* 2004). In strong support to the supramodal theory proposed by Pietrini and colleagues (2004)

are the findings of a recent fMRI indicating that the both sighted and congenitally blind individuals show the same medial-to-lateral bias for non-living and living stimuli in the ventral temporal extrastriate cortical regions (Mahon *et al.* 2009).

#### 2.4. ...*To spatial perception...*

These findings in the ventral temporal cortex of the ‘what’ pathway in the brain have prompted us to ask whether a similar *supramodal* functional organization also exists in the ‘where’ pathway of the dorsal occipito-parietal stream, involved in spatial processing.

To investigate this question, we have conducted a series of experiments using fMRI and repetitive TMS in sighted and in congenitally blind individuals. In a first study, we measured brain activity while sighted and congenitally/early blind subjects performed a one-back spatial discrimination task of visually and/or tactilely presented matrices. Stimuli consisted of two-dimensional 5x5 matrices and three-dimensional 3x3x3 matrices. White squares and cubes with three or five black target squares or cubes represented the two and three-dimensional visual matrices, respectively. Equivalent two and three-dimensional tactile matrices were wooden squares and cubes with three or five Velcro-covered targets. Subjects were asked to indicate whether the presented matrix was the same or different as compared with the previous one. During the tactile spatial discrimination task, both sighted and blind individuals activated a fronto-parietal network, that extended bilaterally from dorsolateral prefrontal and anterior cingulate cortex towards fronto-parietal sensorimotor and posterior parietal cortical regions, including precuneus and intraparietal sulci (Ricciardi *et al.* 2006; Bonino *et al.* 2008; see Figure 2). A similar fronto-parietal network was activated during the visual version of the spatial task in the sighted subjects (Ricciardi *et al.* 2006). Thus, recruitment of the dorsal cortical pathway in response to the tactile spatial discrimination task also occurs for non-visual spatial tasks not only in sighted but also in individuals who have never had any visual experience. Altogether, these findings indicate that neural response during non-visual spatial tasks in the dorsal cortical pathway is not mediated by visual-based imagery and that visual experience is not a prerequisite for the development of a more abstract functional organization of the dorsal stream.

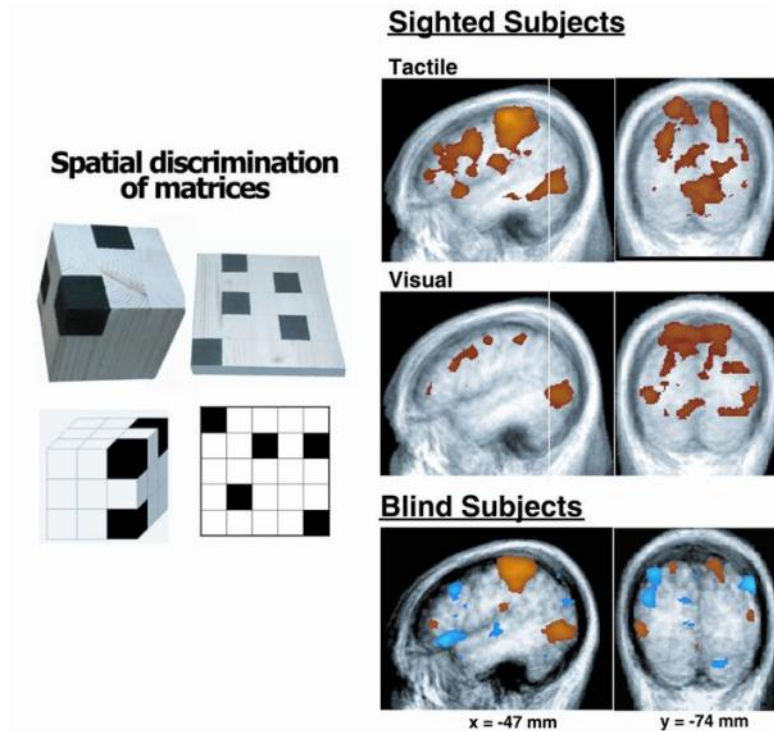


Figure 2. Brain areas that responded during visual and/or tactile spatial discrimination of bi- and tri-dimensional matrices in sighted and congenitally blind subjects. Sagittal and coronal images from group Z-score maps of activated areas are shown (modified from Ricciardi et al. 2006 and Bonino et al. 2008)

### 2.5. ...To spatial imagery...

Given that spatial visual perception and visual imagery engage common cortical areas in the occipito-parietal cortex, we asked whether also spatial imagery may rely on supramodal neural mechanisms, and whether the lack of visual experience may lead blind individuals to employ different cognitive mechanisms as compared to sighted persons (Bonino *et al.* 2010). We examined brain activity in a group of sighted and congenitally/early blind subjects while they performed a modified version of the mental clock test (MCT) (Paivio 1971) under three distinct conditions: auditory-based imagery and visual and/or tactile perception of angle representation. During the auditory-based imagery condition, subjects were asked to imagine two analogue clock faces showing the times that the examiner verbally indicated, and to judge in which case the clock hands formed the wider angle. During the tactile-based and visual-based

perception of angles, participants sequentially compared pairs of clock faces tactilely or visually (sighted subjects only), to decide which hand set formed the wider angle (Figure 3).

Behaviourally, during the auditory-based imagery condition sighted participants showed a significantly higher accuracy as compared to blind individuals. At a functional level, during the auditory imagery condition, both sighted and congenitally blind individuals showed significant activations in posterior parietal areas, including the intraparietal sulcus and the inferior parietal lobule. These same areas showed significant activations also during the tactile and visual angle discrimination conditions in both groups. As expected, auditory, visual and tactile primary sensory regions also were activated during the respective experimental conditions. In a direct group comparison, blind individuals showed a greater activation in bilateral middle and medial occipital areas during both auditory-driven imagery and tactile perception conditions (Bonino *et al.* 2010).

These results provide strong evidence that both in sighted and congenitally blind individuals spatial imagery recruits posterior parietal extrastriate cortex, including the dorsal stream, independently from the sensory modality through which they have acquired spatial experience since the first days of life. Furthermore, congenitally blind individuals showed a greater recruitment of early occipital areas during both auditory spatial imagery and tactile spatial perception. Interestingly, the sighted group activated more task-related posterior parietal areas in the auditory-based imagery condition, during which they had a greater accuracy than the blind subjects. Thus, while lack of visual experience does not preclude an efficient spatial imagery nor the *supramodal* organization of the dorsal stream, sighted and congenitally blind individuals show differences both at a behavioural and a neural level in response to spatial imagery tasks.

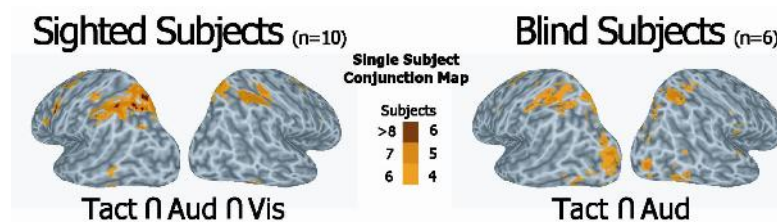


Figure 3. *Conjunction maps overlapping individual subject responses to tactile, auditory and visual (sighted only) stimuli during a modified version of the mental clock task. In both sighted and congenitally blind individuals, auditory-based spatial imagery recruited bilateral posterior parietal cortex, including regions of the dorsal extrastriate stream. The same regions were recruited also during tactile and, in the sighted subjects, visual perception of clock face angles*

The above results are in accordance with findings from an independent study by Vanlierde *et al.* (2003) who, by using PET to measure regional cerebral blood flow, showed activations in precuneus, superior parietal cortex and occipital areas in early blind and sighted volunteers during the mental representation of verbally provided bi-dimensional patterns placed in a grid and the assessment of pattern symmetry in relation to a grid axis. Consistent results have been reported also for spatial localization tasks of auditory stimuli in blind individuals (Gougoux *et al.* 2005; Voss *et al.* 2006).

#### 2.6. ...*The key feature is supramodality*

As a whole, these studies indicate that the ‘visual’ extrastriate association cortical regions are capable of processing information carried by non-visual sensory modalities (Pietrini *et al.* 2009; Struiksma *et al.* 2009). Importantly, this ability is not merely the consequence of a phenomenon of plastic functional reorganization in the brain of subjects deprived of sight since birth or soon afterwards, as this ability also exists in sighted subjects. Not surprisingly, however, sighted and congenitally blind individuals do show differences both at a behavioural and functional level. Differences in the extension and magnitude of the activation of the recruited areas are likely due to the effects of rearrangements that follow the lack of sight, as well as to the different strategies utilized by sensory-deprived individuals (Pietrini *et al.* 2009; Fiehler *et al.* 2010; Matteau *et al.* 2010).

The *supramodal* nature of this functional cortical organization may explain how individuals who have never had any visual experience are able to acquire normal knowledge about objects and their position in space, form mental representations of and interact effectively with the external world.

#### 2.7. *Moving in space by sight, touch or hearing: does it matter for the brain?*

An efficient interaction with the external world requires the ability to perceive dynamic changes from the complex sensorial input and react promptly. This requires the efficient processing of motion in space. Is the information on motion perception processed also in a *supramodal* fashion? And which is the effect of visual experience on the development of functional architecture in motion responsive cortical regions?

Perception of dynamic stimuli in the visual and tactile sensory modalities share fundamental psychophysical aspects that can be explained by similar computational models: both optic and tactile motion provide information

about object form, position, orientation, consistency and movement, as well as information about the position and movement of the self in the environment (Bicchi *et al.* 2008).

In humans, visual perception of motion activates a specific circuit within the temporo-occipital cortical regions that classically includes the middle temporal complex, hMT+ (Watson *et al.* 1993; Zeki *et al.* 1993; Tootell *et al.* 1995). This extrastriate visual cortical area is activated also during apparent and illusory visual motion, and mental imagery of movement (Tootell *et al.* 1995; Goebel *et al.* 1998; Kourtzi and Kanwisher 2000; Mather *et al.* 2008).

Moreover, hMT+ responds to the perception of auditory and tactile motion in sighted (Hagen *et al.* 2002; Ricciardi *et al.* 2007; Summers *et al.* 2009; Ptito *et al.* 2009), as well as in congenitally blind individuals (Poirier *et al.* 2006; Ricciardi *et al.* 2007). These latter findings indicate that hMT+ also processes non-visual sensory inputs of motion, that its recruitment is not simply mediated by visual-based mental imagery and that visual experience is not a prerequisite for the development of the functional organization of this motion-responsive area (Figure 4).

Visual experience, however, does lead to a functional segregation within hMT+. We compared functional brain response in sighted subjects and in individuals with congenital or early blindness during passive perception of visual and/or tactile motion. Visual motion stimuli consisted of grey dots on a black background whereas tactile motion stimuli were made of Braille-like raised dots on a plastic surface moving horizontally or rotationally (Ricciardi *et al.* 2007). Indeed, tactile motion perception in sighted subjects activated the more anterior portion of visual motion-responsive regions but deactivated the more posterior subregion that was activated by visual motion only. By contrast, perception of tactile motion in congenitally blind subjects activated the full extent of hMT+, including the more posterior part. Analogous results have been reported for auditory discrimination of motion (Poirier *et al.* 2006) and for electrotactile motion stimulation of the tongue in sighted and in congenitally blind individuals (Matteau *et al.* 2010). In line with these findings, the results of an fMRI study by Beauchamp *et al.* (2007) demonstrated that the anterior and dorsal middle-superior temporal area (MST), but not the remaining portion of hMT+, responded to simple vibrotactile stimuli.

Recently, repetitive transcranial magnetic stimulation (rTMS) was used to determine whether this more anterior portion of hMT+ truly plays a functional role in tactile motion processing. In blindfolded sighted individuals who were asked to tactilely detect changes in the velocity of a random Braille-like dot pattern with the tip of their index and middle fingers, accuracy and reaction times were significantly impaired only when rTMS was applied on the more anterior part of hMT+, but not on a control parieto-occipital area (Ricciardi *et*

*al.* 2010). These results indicate that hMT+ recruitment is not an epiphenomenon but is truly necessary for tactile processing of motion, and provide additional evidence to the hypothesis of a supramodal functional organization for the more anterior part of this sensory motion processing area.

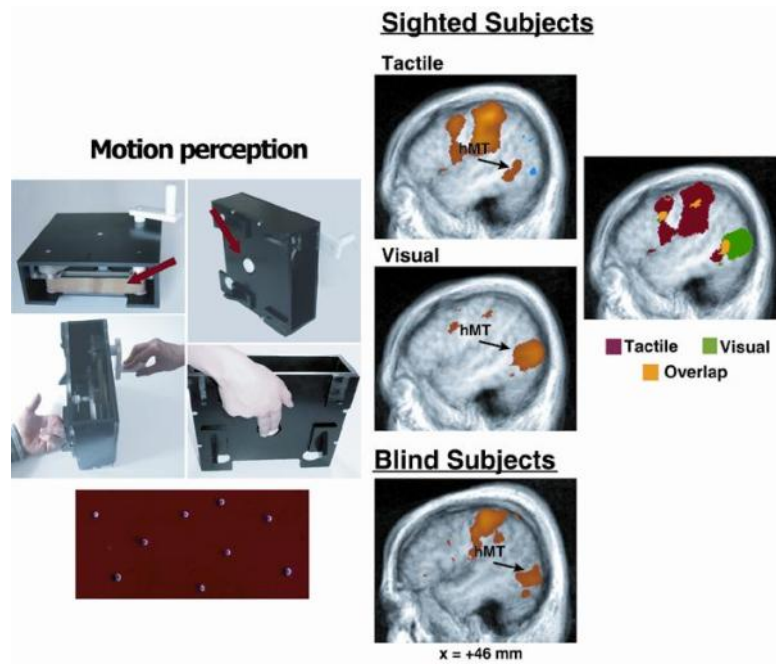


Figure 4. Brain areas that responded during visual and/or tactile motion perception in sighted and congenitally blind subjects. Sagittal images from group Z-score maps of activated areas are shown. The human middle temporal complex (hMT+) activated by tactile and/or visual motion perception is indicated. The tactile/visual overlap map shows the areas activated by both tactile and visual motion (shown in yellow), as well as the areas activated only by tactile (red) and visual (green) perception in the sighted individuals. The right part of the figure shows the device used to administer rotational and translational tactile motion stimuli to the subject's fingers (modified from Ricciardi et al. 2007)

## 2.8. Spatial navigation in the absence of vision

Vision is undisputedly an ubiquitous facilitator of navigation. The access to visual information is critical for updating one's position relative to space and for providing distant spatial cues at a glance. Avoiding obstacles and creating a cognitive map of the environment is obviously more difficult in the absence of vision and remains one of the greatest navigational challenges faced by blind individuals. Nonetheless, most studies investigating navigational skills within

large scale environments such as buildings, obstacle courses and human-size mazes concur that congenitally blind subjects are better than blindfolded seeing controls in orienting themselves inside such complex environments (Fortin *et al.* 2008; Chebat *et al.* 2010). For instance, Chebat *et al.* (2010) reported that congenitally blind subjects outperformed blindfolded sighted controls in avoiding obstacles within a life-size obstacle course, using the tongue display unit (TDU), a sensory substitution device which translates visual images into electrotactile stimulation of the tongue (Bach-Y-Rita and Kerckel 2003; Ptito *et al.* 2005). There is evidence that congenitally blind people are able to understand space at each of the three levels of cognitive structure, namely the enactive representation centered on motor responses, the iconic representation based on mental imagery and the symbolic representation supported by language (Hart and Moore 1973). In generating spatial representations, blind subjects rely on tactile, auditory and olfactory cues, as well as on motion-related cues arising from the vestibular and proprioceptive systems (Strelow and Brabyn 1982; Passini *et al.* 1990). Echolocation is also of great importance and is efficiently used by the blind to estimate object distance, size, density and even texture (Kellogg 1962). Thereby, blind subjects first scan the environment by producing a sound with their cane, fingers, foot or voice, and then listen binaurally to the returned sound waves.

It has been hypothesized that the superior performance of congenitally blind subjects compared to their blindfolded sighted counterparts is due to their more efficient use of proprioceptive signals and environmental cues such as temperature and echolocation. When access to these cues is limited, blind subjects lose their advantage. This is illustrated in a recent study by Gagnon *et al.* (2010) showing that blindfolded sighted controls outperformed blind participants in learning to navigate through small-scale, tactile multiple T-mazes which dramatically limit the use of environmental cues.

An important issue concerns the cortical network that is recruited by navigation in blind subjects. The neural correlates of navigation in the absence of vision have remained largely elusive, mainly because of the difficulty in testing navigational skills of blind subjects in a functional brain imaging study. Kupers *et al.* (2010) recently circumvented this difficulty by using the TDU. They trained a group of congenitally blind and blindfolded sighted participants to navigate through two virtual routes that were presented via the TDU. Once fully trained, subjects repeated the navigation task inside the MRI scanner. During route navigation, blind subjects showed increased neural responses in large parts of the visual cortex, the right parahippocampus, posterior parietal cortex, precuneus and dorsolateral prefrontal cortex (Figure 5). These data are in sharp contrast with those of the blindfolded sighted controls who activated the precuneus and posterior parietal and prefrontal cortices but not the

parahippocampus or visual cortex. A second fMRI experiment by the same authors demonstrated that the areas activated by the blind participants are the same as those activated by sighted subjects when they did the same navigational task under full vision. These data suggest cross-modal plasticity in spatial coding (e.g. Wittenberg *et al.* 2004; Kupers *et al.* 2006; Ptito and Kupers 2005; Ptito *et al.* 2009; Pietrini *et al.* 2009). They also suggest that visual experience is not necessary for the development of spatial navigation network in the brain, as visual association cortical areas are capable of processing and interpreting spatial information carried by non-visual sensory modalities.

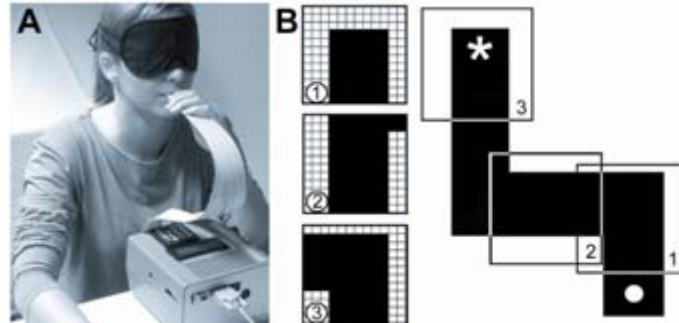


Figure 5. *A. Experimental set-up showing a participant equipped with the tongue display unit.*  
Figure 5. *B. One of the two virtual routes that were used in the navigation task. The position of the subject in the trail and the end of the trail are represented by respectively the white dot and the asterisk. At any given time, only a part of the routes was “visible” to participants as illustrated by snapshots of the spatial layout within three route segments (indicated by the numbers 1-3)*

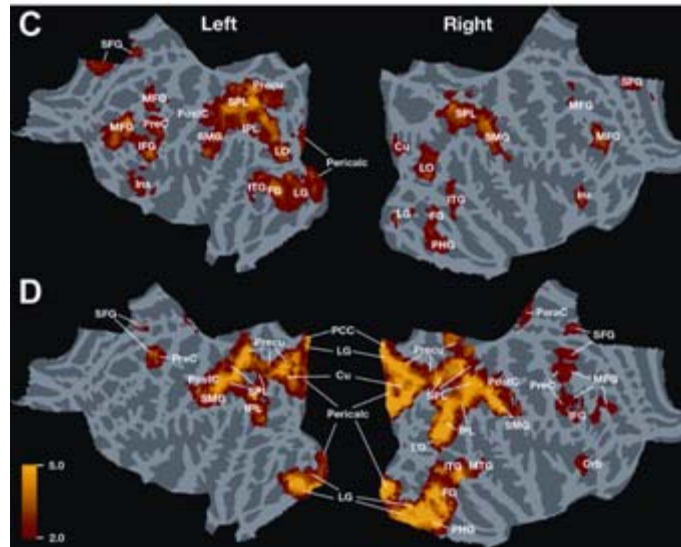


Figure 5. C. Results of blind participants, showing activation of occipital and posterior parietal cortices, precuneus, fusiform gyrus and right parahippocampus during route recognition with the TDU.

Figure 5. D. Sighted control subjects performing the route recognition task visually showed strong activation in the occipital and superior parietal cortices, the precuneus, fusiform gyrus and right parahippocampus. Abbreviations: Cu: Cuneus; FG: fusiform gyrus; Ins: insula; IFG: inferior frontal gyrus; IPL: inferior parietal lobule; ITG: inferior temporal gyrus; LG: lingual gyrus; LO: lateral occipital; MFG: middle frontal gyrus; MTG: middle temporal gyrus; Orb: orbital gyrus; Paracent: paracentral gyrus; Pericalc: pericalcarine sulcus; Precent: precentral gyrus; Precun: precuneus; Postcent: postcentral gyrus; SFG: superior frontal gyrus; STG: superior temporal gyrus; SPL: superior parietal lobule; SMG: supramarginal gyrus (modified from Kupers et al. 2010)

### 2.9. Spatial number and action representation

Several cognitive and motor functions (such as mathematics and action control) rely on a mental spatial representation in sighted individuals. Recent studies have also indicated that people deprived of visual experience show a spatial organization of number representation similar to sighted individuals, suggesting that also number representation may be independent from the sensory input. Indeed, early visual deprivation does not seem to preclude the development of a comparable spatial continuum oriented from left to right to represent numbers, and of even better mapping abilities between the symbolic representation of numbers and their corresponding magnitude (Szűcs and Csépe 2005; Castronovo and Seron 2007). For instance, in a number

comparison task during which subjects were asked to decide whether digits were smaller or larger than five, blind individuals showed a numerical distance effect similar to sighted individuals: reaction times were longer and accuracy was worse when discriminating numerically closer than further apart quantities (Szűcs and Csépe 2005).

Consistently, this supramodal mental number line has been shown to exert an influence on the visuospatial allocation of attention (Dahene *et al.* 2003), and on the representation of peripersonal haptic space (Cattaneo *et al.* 2010). Recent electrophysiological and TMS experiments indicate a critical involvement of the intraparietal sulcus and the angular gyrus of the posterior parietal cortex in numerical cognition (Brannon 2006; Szűcs and Csépe 2005; Cattaneo *et al.* 2009).

Similarly, spatial processing and the posterior parietal cortex play a fundamental role in action planning and control, specifically in determining “how” to interact with and manipulate an object (Fiehler *et al.* 2010). Recently, Fiehler *et al.* (2009) found a large activation overlap in areas of the dorsal pathway for congenitally blind and sighted participants during performance of kinaesthetically guided hand movements (e.g., while subjects performed active and passive hand movements without any visual feedback), thus confirming the function of the dorsal occipito-parietal regions in online action control and representation. In contrast to the sighted participants, congenitally blind participants additionally activated ventral extrastriate regions and the auditory cortex. These findings indicate that action control is subserved by a *supramodal* network that develops on the basis of sensorimotor feedback rather than being under the exclusive control of vision. Moreover, the differential involvement of ventral extrastriate and auditory regions indicates that visual deprivation results in a cross-modal compensatory plastic recruitment. These findings are consistent with other reports that congenitally blind subjects performed similarly to those with acquired blindness and that early visual experience is not necessary to perform many tasks of action control (e.g. Vanlierde and Wanet-Defalque 2004).

### 3. CONCLUSIONS

Although vision offers distinctive information to the representation of the surroundings and to item localization, individuals who are visually-deprived since birth show spatial discrimination and navigational skills that are significantly comparable to those in sighted individuals, even for those cognitive domains that rely on mental spatial representation, such as number processing or action planning.

The main findings on spatial mental representation in blind individuals extend to the dorsal extrastriate cortical pathway, that processes spatial and motion-related information, the *supramodal* functional organization previously demonstrated in the ventral temporal cortical pathway for object categories discrimination (Pietrini *et al.* 2004, 2009; Mahon *et al.* 2009). Moreover, sighted and congenitally blind individuals showed also differential regional activations, indicating that while lack of vision does not affect significantly the development of the main functional architecture of the brain, at the same time it does lead to some functional rearrangements in vision-related cortical areas. The investigation of the differential brain regional susceptibility to the lack of vision may deepen our understanding of which portion of the morphological and functional development of the human brain is pre-determined and independent from visual experience and, conversely, which neural processes are molded by vision.

Altogether, behavioural and functional studies on spatial cognition in blind individuals have provided novel and unexpected insights on many questions regarding not only the plastic rearrangements that take place when vision is absent but, *in primis*, on the functional organization of the sighted brain itself. The availability of sophisticated in vivo brain functional methodologies has made it possible to begin to understand the neural mechanisms that enable humans to obtain a conscious representation of and interact efficiently with the external world.

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