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Spatial imagery relies on a sensory independent, though sensory sensitive, functional organization within the parietal cortex: A fMRI study of angle discrimination in sighted and congenitally blind individuals

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ABSTRACT

Although vision offers distinctive information to space representation, individuals who lack vision since birth often show perceptual and representational skills comparable to those found in sighted individuals. However, congenitally blind individuals may result in impaired spatial analysis, when engaging in 'visual' spatial features (e.g., perspective or angle representation) or complex spatial mental abilities. In the present study, we measured behavioral and brain responses using functional magnetic resonance imaging in sighted and congenitally blind individuals during spatial imagery based on a modified version of the mental clock task (e.g., angle discrimination) and a simple recognition control condition, as conveyed across distinct sensory modalities: visual (sighted individuals only), tactile and auditory. Blind individuals were significantly less accurate during the auditory task, but comparable-to-sighted during the tactile task. As expected, both groups showed common neural activations in intraparietal and superior parietal regions across visual and non-visual spatial perception and imagery conditions, indicating the more abstract, sensory independent functional organization of these cortical areas, a property that we named *supramodality*. At the same time, however, comparisons in brain responses and functional connectivity patterns across experimental conditions demonstrated also a functional lateralization, in a way that correlated with the distinct behavioral performance in blind and sighted individuals. Specifically, blind individuals relied more on right parietal regions, mainly in the tactile and less in the auditory spatial processing. In sighted, spatial representation across modalities relied more on left parietal regions. In conclusions, intraparietal and superior parietal regions subserve *supramodal* spatial representations in sighted and congenitally blind individuals. Differences in their recruitment across non-visual spatial processing in sighted and blind individuals may be related to distinctive behavioral performance and/or mental strategies adopted when they deal with the same spatial representation as conveyed through different sensory modalities.

1. Introduction

Since the pivotal studies by Kosslyn in the seventies (e.g., Kosslyn, 1973), there is ample evidence that chronometric properties of mental images are shared with visual percepts. The role of vision in shaping and modulating these functions, as well as in influencing the development of the neural structures underlying these abilities, however, remains still to be fully defined.

Although vision offers distinctive information for the representation of the surroundings, so that for a long time it has been thought to be crucial for the development of spatial abilities, a growing body of evidence suggests that the lack of visual experience may have just limited effects on the perception and mental representation of space (Cattaneo et al., 2008; Ricciardi et al., 2010). As a matter of fact, individuals who are

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visually-deprived since birth show similar levels of performance to sighted individuals in distinct spatial discrimination tasks, including navigation, number processing or action planning (Aleman et al., 2001; Cattaneo and Vecchi, 2011; Fleming et al., 2006; Ricciardi et al., 2010; Vecchi, 1998).

Neuropsychological, lesion and functional brain studies indicate that spatial perceptual abilities and spatial mental representations critically rely on posterior parietal regions (Ricciardi et al., 2010; Sack et al., 2002a, 2002b; Trojano et al., 2002, 2000). Interestingly, these cortical regions are activated during both perceptual and imagery tasks, regardless of the sensory modality through which such a spatial information has been acquired (Cattaneo et al., 2008; Ptito et al., 2011; Ricciardi et al., 2014a, 2014b, 2010; Ricciardi and Pietrini, 2011). Furthermore, congenitally blind individuals recruit intraparietal and superior parietal regions during non-visual spatial processing and localization (Weeks et al., 2000), spatial imagery (Vanlierde et al., 2003), orientation discrimination (Ptito, 2005), spatial attention and memory (Bonino et al., 2008), and even numerical comparison (Szucs and Csepe, 2005) tasks. Altogether, these observations strongly suggest a more abstract, visual-independent sensory representation of spatial information in the human brain, that is, a *supramodal* functional organization.

On the other hand, blind individuals do acquire a reduced amount of sensorial information, in terms of both classical 'visual' spatial features (e.g., perspective or angle representation) and their simultaneous and integrated perception, as compared to sighted ones (Cattaneo and Vecchi, 2008). At a behavioral level, these perceptual limitations result in impaired responses when individuals perform spatial imagery tasks that rely on visually-based representations, or that involve complex spatial mental abilities (Cattaneo et al., 2008; Gori et al., 2014; Struiksma et al., 2009). For instance, performance differed between congenitally blind and sighted participants in a spatial-imagery task of angle discrimination, but not in a visually-based or auditory-based imagery tasks of object form (Noordzij et al., 2007). Similarly, dealing with multiple or three-dimensional spatial mental representations may be rather problematic for congenitally blind individuals (Vecchi, 1998; Vecchi et al., 1995). Indeed, blind individuals develop their cognitive mechanisms through touch and hearing, which only allow for a sequential processing of information. This may force people who lack vision since birth to rely, at a higher cognitive level, on partially different non-visual spatial processes (Noordzij et al., 2007; Vecchi, 1998).

At a neural level, brain responses across distinct perceptual tasks in sighted and congenitally blind individuals show both similar patterns of activation within wide portions of association cortical areas (Ricciardi et al., 2014a) and a differential recruitment of primary visual cortical areas (Vanlierde et al., 2003), due to cross-modal plastic functional rearrangements in vision-related cortical areas (Kupers et al., 2011a; Ricciardi and Pietrini, 2011). Overall, these findings indicate that in the brain *supramodal* and *cross-modal* functional organizations coexist. As a matter of fact, we can think of the two phenomena as of the two sides of the same coin: *supramodality* is the functional architecture that takes place *despite* the lack of visual input, whereas *cross-modal plasticity* is the functional rearrangement that occurs *because of* the lack of sight (Ricciardi et al., 2014a, 2014b).

In the present study, we wished to examine to what extent (the lack of) visual experience and the specific features of the distinct sensory modalities may affect the brain functional architecture that sustains spatial imagery. Specifically, we measured brain responses in both sighted and congenitally blind individuals during an angle discrimination task in which stimuli were presented through the visual (sighted subjects only), tactile and auditory pathways. Previous studies showed that in sighted individuals angle size detection relies on a bilateral, though left-dominant, recruitment of posterior parietal regions (Formisano et al., 2002; Trojano et al., 2000). Further, at a behavioral level, congenitally blind individuals showed significantly lower degrees of performance in a spatial-imagery task of angle discrimination as compared to sighted ones (Noordzij et al., 2007).

Based on the observations discussed above, we predicted that spatial imagery would be associated with a shared *supramodal* functional response within the parietal cortical areas related to spatial perception, that is, this area would be recruited independently from visual experience and from the sensory channel used for angle spatial perception. At the same time, given the distinctive features of mental processing, as well as previous findings from distinct studies on spatial perception in sighted and congenitally blind individuals obtained in our own lab (Bonino et al., 2008; Ricciardi et al., 2006, 2007), we also expected that within this common *supramodal* functional architecture, patterns of neural response would be shaped to some extent by visual experience and by the distinctive features of the specific sensory modality utilized to acquire spatial information.

2. Materials and methods

2.1. Subjects

We measured neural activity in 10 sighted (7M/3F, mean age ± s.d. = 29 ± 3 years) and nine congenitally blind (5M/4F, 43 ± 16 years; age group comparison, *t*-test Bonferroni corrected, p = n.s.) right-handed healthy volunteers. Eight subjects were blind from birth, and one became totally blind by the age of 18 months (she lost the right eye vision at 10 months, and the left eye vision at 18 months) and had no recollection of any visual memory. Only individuals with a peripheral cause of congenital blindness were admitted to the study. In order to avoid any possible bias due to the familiarity with the task (e.g. Noordzij et al., 2007), we selected only sighted and congenitally blind volunteers who had experience of analogical or traditional tactile Braille clocks, respectively. Due to significant head movement artifacts (greater than one voxel sixe), three congenitally blind individuals had to be dismissed, so that data from six congenitally blind (4M/2F, 39 ± 16 years; age group comparison, Bonferroni corrected p = n.s.) volunteers entered the behavioral and brain functional data analysis. Causes of blindness for each of the six individuals are reported in Table 1.

All sighted and blind participants received a clinical examination, including routine blood tests and a brain structural MRI scan, to exclude any disorder that could affect brain function or metabolism, other than blindness in the blind group. No subject was taking any psychotropic medication. All participants gave their written informed consent after the study procedures and potential risks had been explained. The study was conducted under a protocol approved by the Ethical Committee at the University of Pisa

Table 1
Characteristics of the congenitally blind volunteers enrolled in the study.

Gender	Age (years)	Age of blindness onset (months)	Cause of blindness
Male	31	0	Congenital glaucoma
Male	58	0	Congenital glaucoma
Male	53	0	Congenital optic atrophy of unknown cause
Female	42	0	Retinopathy of prematurity
Female	20	18	Congenital glaucoma
Male	57	0	Congenital cataract