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Review

Mind the blind brain to understand the sighted one! Is there a supramodal cortical functional architecture?

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ABSTRACT

While most of the research in blind individuals classically has focused on the compensatory plastic rearrangements that follow loss of sight, novel behavioral, anatomical and functional brain studies in individuals born deprived of sight represent a powerful tool to understand to what extent the brain functional architecture is programmed to develop independently from any visual experience. Here we review work from our lab and others, conducted in sighted and congenitally blind individuals, whose results indicate that vision is not a mandatory prerequisite for the brain cortical organization to develop and function. Similar cortical networks subtend visual and/or non-visual perception of form, space and movement, as well as action recognition, both in sighted and in congenitally blind individuals. These findings support the hypothesis of a modality independent, *supramodal* cortical organization. Visual experience, however, does play a role in shaping specific cortical sub-regions, as loss of sight is accompanied also by *cross-modal* plastic phenomena. Altogether, studying the blind brain is opening our eyes on how the brain develops and works.

Contents

1. Is vision the only way "to see"?

When observing a blind individual, people may find themselves wonder whether that person is really visually-deprived. Indeed, individuals who lack vision are proficient in everyday's life activities, are able to interact efficiently with the surrounding objects and tools, move independently in space, and interact socially with others. Although vision offers distinctive information, several observations indicate that the lack of visual experience may have just limited effects on the perception and mental representation of the surrounding world. As a matter of fact, some blind individuals may even excel in activities that would be considered strictly visual: Esref Armagan (www.armagan.com/), John

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Bramblitt and Sargy Mann are painters; Michael Naranjo and Steve Handschu are sculptors; Kurt Weston, Evgen Bavcar and Peter Eckert (http://www.peteeckert.com/) are photographers. These are just a few world-known examples of artists who rely on non-visual sensory esthetic to create and make people appreciate a 'visual' beauty. Moreover, blind individuals very often may make sighted individuals notice some specific sensorial aspects that the latter are simply 'unable to see'.

Indeed, vision plays a primary role in how we represent and interact with the world around us. 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. Furthermore, from a neuro-anatomical perspective, approximately 55% of the whole cortex in primates is devoted to visual function, as compared to only 3% for auditory processing and 11% for somatosensory processing (Felleman and Van Essen, 1991). Nonetheless, as mentioned before, vision is not necessary to "see" the world around us, and to form a proficient mental representation of it. In particular, blind individuals who have been visually-deprived since birth show cognitive and social skills that are substantially comparable to those in sighted individuals (Cattaneo et al., 2008; Kupers et al., 2011; Noppeney, 2007). On the other hand, several studies have shown that lack of visual experience often delays the physiological development of cognitive, social and linguistic skills in blind children (Fraiberg, 1997; Peterson et al., 2000; Tobin, 1998) and affect their social functioning. Moreover, while cases of congenitally blindness have decreased significantly over the last decades in the Western countries, both congenital blindness in the developing areas and acquired blindness still represent a major public health issue, as they affect millions of individuals worldwide (http://www.who.int/mediacentre/factsheets/fs282/en/).

In the last years, functional brain studies of visually-deprived individuals have offered a unique tool to examine the role of visual experience in forming a representation of the world, as well as to understand to what extent vision is a mandatory prerequisite for the human brain to develop and function. Congenitally blind individuals have provided novel and stimulating insights on many questions regarding not only the cross-modal plastic rearrangements that inevitably take place when vision is absent, but primarily the functional development and organization of the sighted brain itself.

2. To what extent is vision really necessary for the human brain to develop and function?

2.1. Supramodal cortical organization subtends a more abstract representation

In order to disentangle how the human brain represents the surrounding world through non-visual sensory modalities, distinct functional brain studies have explored how pieces of information conveyed by touch, hearing, smell or taste, are processed in sighted individuals (e.g. Amedi et al., 2005c; Peelen et al., 2010; Ricciardi et al., 2006). Though many studies reported significant overlapping activations in visual processing areas during these non-visual perception tasks, and thus were in line with the hypothesis of a more abstract representation of the perceived stimuli in 'visual' areas (Amedi et al., 2005a, 2005c; Lacey et al., 2007; Pascual-Leone and Hamilton, 2001), they could not rule out that these 'visual' activations merely be the effect of the recall of visual imagery-based mental representations (Ricciardi and Pietrini, 2011). Indeed, several independent reports have shown a remarkable similarity in the brain neural response elicited by perception and imagery of the same object category (Ishai, 2010; Ishai et al., 2000).

A crucial advancement in the demonstration of a *supramodal* functional cortical organization in the human brain came from the study of visually-deprived individuals, who were either congenitally blind or had become blind at a very early age, and had no visual memories. Indeed, functional brain studies in individuals who have had no vision-based experience or representation made it possible for the first time to demonstrate that neural responses in visual cortex during non-visual sensory processing are not due to visual imagery process (Pietrini et al., 2004). Furthermore, these studies in congenitally blind individuals have been instrumental to understand to what extent visual experience is a mandatory prerequisite for the brain to develop its morphological and functional organization within these "visual" cortical regions. At the same time, if a given feature is also present in sighted individuals, its functional recruitment in congenitally blind individuals has to reflect a more abstract, supramodal representation of a specific content of information, either structurally or semantically, and cannot be simply a consequence of a plastic rearrangement due to the lack of vision (Pietrini et al., 2004, 2009; Ricciardi and Pietrini, 2011).

To date, several perceptual, cognitive and, more recently, affective domains have been explored in congenitally blind individuals by combining functional brain imaging methodologies with distinct experimental paradigms. As summarized in Table 1 and Fig. 1, these findings provide a consistent demonstration of the supramodal functional organization of specific task-related cortical networks. For instance, relatively to the well-known organization of the visual system into specialized subregions and distinctive streams of information processing (e.g., the 'what', ventral vs. the 'where/how', dorsal pathways – Milner and Goodale, 2008; Ungerleider and Haxby, 1994), object representation, motion discrimination and spatial localization have been the most explored abilities. A similar supramodal functional organization for both the ventral temporal occipital cortex of the 'what' pathway and the dorsal occipito-parietal stream of the 'where/how' pathway has been shown to process, respectively, object form and spatial perception and imagery regardless of the sensory modality through which the information had been acquired, in both sighted and blind individuals (Bonino et al., 2008; De Volder et al., 2001; Lambert et al., 2004; Pietrini et al., 2004; Ricciardi et al., 2010; Vanlierde et al., 2003; Weeks et al., 2000). Thus, highly specialized visual areas, such as the human middle temporal complex (hMT+) or the parahippocampal gyrus, maintain their functional specificity, that is, respectively, motion processing and spatial layout coding, when information are provided through non-visual stimulation tasks, such as tactile or auditory paradigms (Poirier et al., 2006; Ptito et al., 2009; Ricciardi et al., 2007).

Interestingly, the functional specificity of this supramodal recruitment in both sighted and blind individuals has been confirmed by many distinct experimental protocols that either conveyed information across different non-visual sensory modalities or via sensory substitution devices, or impaired selective processing by 'virtual' (via transcranic magnetic stimulation - TMS) lesions (Collignon et al., 2011a; Frasnelli et al., 2011; Kupers et al., 2011; Kupers and Ptito, 2011; Noppeney, 2007). In addition, connectivity approaches (Klinge et al., 2010; Ma and Han, 2011; Sani et al., 2010; Wolbers et al., 2011), or correlations with behavioral performances (Amedi et al., 2003) further contributed to validate the functional homologies between sighted and blind individuals.

A representative case to summarize this experimental route is provided by the studies of object and shape perception. In sighted individuals, visual recognition of distinct object categories elicits distributed and overlapping patterns of neural response in the ventro-temporal extrastriate cortical areas (Haxby et al., 2001). This model, named '*object form topology*', raises the question whether such a functional organization is strictly visual or rather represents a more abstract, supramodal functional organization