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Review

Compensatory plasticity and cross-modal reorganization following early visual deprivation

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ABSTRACT

For human and non-human primates, vision is one of the most privileged sensory channels used to interact with the environment. The importance of vision is strongly embedded in the organization of the primate brain as about one third of its cortical surface is involved in visual functions. It is therefore not surprising that the absence of vision from birth, or the loss of vision later in life, has huge consequences, both anatomically and functionally. Studies in animals and humans, conducted over the past few decades, have demonstrated that the absence of vision causes massive structural changes that take place not only in the visually deprived cortex but also in other brain areas. These studies have further shown that the visually deprived cortex becomes responsive to a wide variety of non-visual sensory inputs. Recent studies even showed a role of the visually deprived cortex in cognitive processes. At the behavioral level, increases in acuity for auditory and tactile processes have been reported. The study of the congenitally blind brain also offers a unique model to gain better insights into the functioning of the normal sighted brain and to understand to what extent visual experience is necessary for the brain to develop its functional architecture. Finally, the study of the blind brain allows us to investigate how consciousness develops in the absence of vision. How does the brain of someone who has never had any visual perception form an image of the external world? In this paper, we discuss recent findings from animal studies as well as from behavioural and functional brain imaging studies in sighted and blind individuals that address these questions.

Contents

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1. Introduction

Traditionally, vision has always been considered as the most important sense for humans to interact with the environment. The relevance of sight is strongly embedded in common linguistic expressions. Consider everyday phrases, such as "I see what you mean" or "Do you see my point?" The importance that vision plays in everyday life is also reflected at the level of cortical organization. Indeed, about one third of the cortical surface in primates is involved in visual functions. This raises the question what happens to the visual cortex, both anatomically and functionally, when vision is lost at birth or later in life. There is now a wealth of animal studies showing that neonatal visual deprivation causes massive structural changes that take place not only in the visually deprived cortex but also in other brain areas (reviewed in Ptito and Desgent, 2006; Desgent and Ptito, 2012). In addition, these animal studies have shown that the visually deprived cortex becomes responsive to a variety of non-visual inputs. More recent studies have confirmed that similar plastic rearrangements also take place in the human brain. Whereas the initial studies focused largely on cross-modal responses in the tactile and auditory domain, more recent studies revealed a broader picture showing that the visually deprived occipital cortex is also involved in processing information from other sensory modalities (Kupers et al., 2011a), and even in various cognitive processes (Amedi et al., 2003, 2004; Bonino et al., 2008; Burton et al., 2003; Cattaneo et al., 2008; Kupers et al., 2007, 2010; Raz et al., 2005; Stevens et al., 2007).

The study of the congenitally blind brain also offers a unique model to gain better insights into the functioning of the normal sighted brain. To what extent is visual experience truly necessary for the brain to develop its functional architecture? For instance, is visual input necessary for the development of the dorsal and ventral visual streams? Another question is to which extent blindness causes a hyperacuity of the remaining senses, and if so, whether this hyperacuity is due to the recruitment of the occipital cortex. A final question that we will address in this review relates to the subjective character of activity in visually deprived cortex. In his monumental treatise "The principals of Psychology", published in 1890, William James wondered whether we would "hear the lightning and see the thunder" if we could splice the nerves so that the excitation of the ear fed the brain centre concerned with seeing, and vice versa. We will review data from recent experimental studies that finally provide the first pieces of answer to this centennial question.

2. Compensatory plasticity

The term "compensatory plasticity" was originally coined to contrast common views that predicted a generalized degradation of sensory functions as a result of early blindness, because vision was viewed as the dominant sense that was needed to calibrate the auditory and tactile senses (Rauschecker, 1995). According to this view, even equal effectiveness of non-visual functions in the blind falls under the original meaning of the term. In current opinion, however, the term compensatory plasticity is more often understood in the sense of "coping with the loss of vision by developing supranormal skills when using one of the remaining senses. Whereas there is overwhelming evidence in favour of the first meaning of the concept of compensatory plasticity, there is a large controversy as to the question whether this also implies that the blind are generally "better" than their sighted counterparts in these non-visual tasks.

In the following, we will review studies of tactile, auditory, olfactory, gustatory and thermal processing in congenitally and late blind individuals. A summary of these results can be found in Table 1.

2.1. Tactile processing

Early behavioural studies on tactile performance in blind subjects provided mixed positive and negative results. A study by Craig (1988) conducted in a small study cohort showed improved tactile letter recognition at the fingertips in blind subjects. A subsequent study by Van Boven et al. (2000) compared grating orientation discrimination in proficient early blind Braille readers and age- and sex-matched sighted controls. The blind participants displayed improved tactile grating orientation discrimination for both the dominant Braille reading finger and the remaining fingers of the dominant hand. Goldreich and Kanics (2003) found similar results in large groups of congenitally blind, late blind, and sighted control subjects. Enhanced tactile acuity for grating orientations was present in both groups of blind participants at the dominant (Braille reading) index finger. A more recent study by Legge et al. (2008) also found higher tactile acuity at the fingertips in blind Braille readers compared to sighted control subjects. Interestingly, whereas tactile acuity declined by nearly 1% per year in the group of sighted, blind subjects showed no age-related decline. In line with the results of Goldreich and Kanics (2003), tactile acuity did not correlate with age-of-onset of blindness. Noteworthy, tactile acuity neither correlated with Braille reading speed, the amount of Braille reading, or the age at which Braille reading was learned (Legge et al., 2008). In contrast to the above mentioned results, some other studies did not find systematic differences between blind and sighted subjects in light touch thresholds, vibratory detection, length discrimination or two-point discrimination, or reported that the advantage of the blind disappeared after the sighted received additional training (Heller, 1989; Grant et al., 2000).

Wong et al. (2011) tested whether the improved tactile acuity in blind subjects is due to the fact that they rely more on tactile experience, or to the fact that lack of vision by itself drives increased tactile acuity. These authors tested grating orientation on the index, middle and ring finger of both the dominant and non-dominant hand, and on the lips in a large cohort of blind subjects with varying degrees of Braille reading experience. The results showed that blind participants outperformed the sighted on the fingers, but not on the lips. Additionally, proficient blind Braille readers performed better with the preferred reading finger than with the other fingers, and their acuity scores on the preferred reading finger correlated with measures of the amount of Braille reading. These results are in line with the tactile experience hypothesis, and suggest that higher tactile spatial acuity in the blind is caused by a stronger reliance on the sense of touch. Our own data on non-haptic tactile perception confirm to a large extent the findings by Wong et al. (2011). We trained blind subjects to discriminate patterns of electro-tactile stimulation that were applied to the tongue by means of a tongue display unit (TDU; Bach-y-Rita and Kercel, 2003). Our data showed that at the group level, congenitally blind and matched sighted

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