Neuroscience 283 (2014) 44–63

REVIEW

REVISITING THE ADAPTIVE AND MALADAPTIVE EFFECTS OF CROSSMODAL PLASTICITY

B. HEIMLER,* N. WEISZ AND O. COLLIGNON

Center for Mind/Brain Sciences (CIMeC), University of Trento, Italy

Abstract—One of the most striking demonstrations of experience-dependent plasticity comes from studies of sensory-deprived individuals (e.g., blind or deaf), showing that brain regions deprived of their natural inputs change their sensory tuning to support the processing of inputs coming from the spared senses. These mechanisms of crossmodal plasticity have been traditionally conceptualized as having a double-edged sword effect on behavior. On one side, crossmodal plasticity is conceived as adaptive for the development of enhanced behavioral skills in the remaining senses of early-deaf or blind individuals. On the other side, crossmodal plasticity raises crucial challenges for sensory restoration and is typically conceived as maladaptive since its presence may prevent optimal recovery in sensory-re-afferented individuals. In the present review we stress that this dichotomic vision is oversimplified and we emphasize that the notions of the unavoidable adaptive/maladaptive effects of crossmodal reorganization for sensory compensation/restoration may actually be misleading. For this purpose we critically review the findings from the blind and deaf literatures, highlighting the complementary nature of these two fields of research. The integrated framework we propose here has the potential to impact on the way rehabilitation programs for sensory recovery are carried out, with the promising prospect of eventually improving their final outcomes.

This article is part of a Special Issue entitled: Brain compensation. For good? **© 2014 IBRO. Published by Elsevier Ltd. All rights reserved.**

Key words: crossmodal plasticity, deafness, blindness, adaptive, maladaptive, behavior.

Contents

INTRODUCTION

One important translational objective of the research focusing on brain plasticity as a consequence of sensory loss (e.g., deafness or blindness) is to disclose the impact of the observed reorganizations on rehabilitation outcomes. During the last two decades, the recruitment of the deafferented sensory cortex by the spared sensory modalities has been repeatedly and consistently documented in blind and deaf adults (see for recent reviews Collignon et al., 2009a; Merabet and Pascual-Leone, 2010; Dormal and Collignon, 2011; Pavani and Röder, 2012; Voss and Zatorre, 2012a; Ricciardi et al., 2013). The noticeable phenomenon of experience-dependent plasticity is generally referred to as *crossmodal plasticity* (Bavelier and Neville, 2002). In describing the crucial relationship between the documented crossmodal reorganizations and behavioral outcomes, two main principles have been promoted, often conceptualizing this relationship as a double-edged sword effect (Merabet et al., 2005).

*Corresponding author. Address: Center for Mind/Brain Sciences (CIMeC), University of Trento, Corso Bettini 31, 38068 Rovereto, Italy. Tel: +39-0464-808708; fax: +39-0464-808602.
E-mail addresses: benedetta.heimler@unitn.it, Benedetta.Heimler@mail.huji.ac.il (B. Heimler).

Abbreviations: CIs, cochlear implants; DCM, dynamic causal modeling; fMRI, functional magnetic resonance imaging; LOC/LOtv, lateral occipital cortex; STS, superior temporal sulcus; TSM, Transcranial Magnetic Stimulation; V1, primary visual cortex; vMMN, visual Mismatch Negativity.

http://dx.doi.org/10.1016/j.neuroscience.2014.08.003
0306-4522/

On one side, crossmodal plasticity is conceived as *adaptive* or *compensatory* for behavior. This conception stems from a series of studies that had successfully linked crossmodal recruitment to behavioral advantages documented in the remaining senses as a consequence of sensory loss (e.g., Amedi et al., 2003; Gougoux et al., 2005; Collignon et al., 2007; Karns et al., 2012; Voss et al., 2014; see for a review Voss et al., 2010).

On the other side, when it comes to sensory restoration outcomes (e.g., cochlear implants (CIs); interventions for bilateral cataract removal), crossmodal plasticity is ultimately considered as a negative predictor for efficient sensory recovery; in other words, it is conceived as *maladaptive* for optimal recovery of the previously missing sensory information. This notion mainly emerges from studies conducted with auditory-restored individuals, which documented a correlation between poor language recovery and persistent crossmodal activations elicited by visual or somatosensory inputs (e.g., Doucet et al., 2006; Buckley and Tobey, 2011; Rouger et al., 2012; Sandmann et al., 2012; Sharma et al., 2014; see for reviews Sharma et al., 2009; Collignon et al., 2011a; Kral and Sharma, 2012; Voss, 2013).

In the present review, we stress the limitations of adopting such an oversimplified dichotomic view of the double-edged sword effect of crossmodal plasticity. In particular we emphasize the possibility that the notion of its unavoidable maladaptive effect for sensory restoration outcomes may be misleading. To this final aim, we will review findings coming from two highly intertwined fields of research, namely, the literature on blindness and deafness. As will emerge in the following sections, the majority of the evidence documenting the *adaptive* effects of crossmodal plasticity in cases of sensory deprivation comes from studies carried out with early-blind people (i.e., individuals born with visual impairment and acquiring total blindness very early in life). Much less evidence is available from studies carried out with early bilateral deaf people (i.e., individuals born deaf and acquiring deafness before language acquisition). Evidence regarding the *maladaptive* effects of crossmodal plasticity for sensory restoration outcomes mainly arises from the literature on deafness and auditory restoration. In this domain, evidence coming from blindness and visual restoration is scarcer. Therefore, merging results acquired from these two distinct sensory-deprived populations is fundamental to extract general principles of crossmodal plasticity phenomena and to develop a common framework regarding the effects of crossmodal reorganization for behavior. In other words, such an integrated framework may provide general principles, which may hold true independently of the sensory modality that is absent (i.e., either vision or audition; Bavelier and Neville, 2002). We will first concisely review the evidence in favor of the adaptive effect of crossmodal plasticity in cases of sensory deprivation. We will then question the notion of the unavoidable maladaptive effects of crossmodal reorganization in cases of sensory restoration, starting with findings from auditory restoration and then moving to initial findings and considerations arising from research on sight restoration.

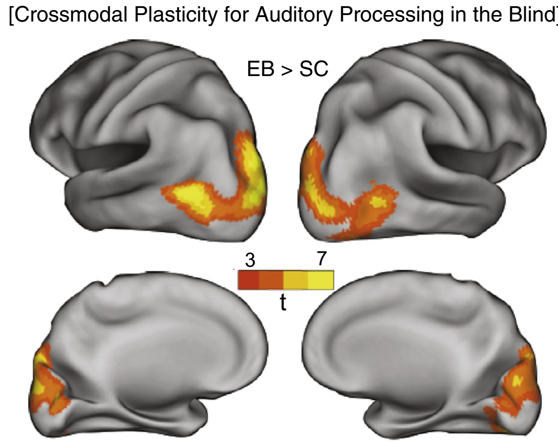

Fig. 1. Example of the massive activation elicited by sounds in the occipital cortex of blind adults. We created this figure using data from Collignon et al. (2011b): it depicts the activation obtained when contrasting early-blind individuals (EB) versus sighted controls (SC) when both groups of participants were exposed to auditory stimuli only.

CROSS-MODAL PLASTICITY IN CASES OF SENSORY DEPRIVATION

Blindness

The occipital cortex of early-blind individuals is massively activated by non-visual inputs (e.g., Collignon et al., 2009a; see Fig. 1). In order to interpret the nature of these crossmodal activations, it was crucial to disambiguate whether they were the effect of a functional remapping of sensory/cognitive functions in the deprived regions, or the product of epiphenomenal or stochastic brain reorganization mechanisms. By now, several pieces of evidence strongly support the former account rather than the latter.

The first piece of evidence in favor of the 'functional remapping account' is supported by the reported case study of an expert blind Braille reader who developed Braille alexia following an ischemic stroke that damaged her occipital cortex bilaterally (Hamilton et al., 2000). Studies using Transcranial Magnetic Stimulation (TMS) further corroborated this possibility by showing that a transient disruption in the activity of occipital regions impairs the behavioral performance in non-visual tasks in early-blind participants, thus strongly supporting the notion of a causal role for the occipital cortex in mediating non-visual processing in early-blind individuals relative to sighted controls (e.g., Cohen et al., 1997; Amedi et al., 2004; Collignon et al., 2007, 2009b; Ricciardi et al., 2011). It has to be acknowledged, however, that there is evidence suggesting that TMS stimulation not only leads to direct effects at the site of stimulation but also affects functionally connected areas that are distant from the stimulation site (Paus et al., 1997; Paus and Wolforth, 1998). In other words, it may be that the drop in behavioral performance that has been repeatedly reported in early-blind participants as a consequence of TMS pulses