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Reading in the dark: neural correlates and cross-modal plasticity for learning to read entire words without visual experience

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ABSTRACT

Cognitive neuroscience has long attempted to determine the ways in which cortical selectivity develops, and the impact of nature vs. nurture on it. Congenital blindness (CB) offers a unique opportunity to test this question as the brains of blind individuals develop without visual experience. Here we approach this question through the reading network. Several areas in the visual cortex have been implicated as part of the reading network, and one of the main ones among them is the VWFA, which is selective to the form of letters and words. But what happens in the CB brain? On the one hand, it has been shown that cross-modal plasticity leads to the recruitment of occipital areas, including the VWFA, for linguistic tasks. On the other hand, we have recently demonstrated VWFA activity for letters in contrast to other visual categories when the information is provided via other senses such as touch or audition. Which of these tasks is more dominant? By which mechanism does the CB brain process reading?

Using fMRI and visual-to-auditory sensory substitution which transfers the topographical features of the letters we compare reading with semantic and scrambled conditions in a group of CB.

We found activation in early auditory and visual cortices during the early processing phase (letter), while the later phase (word) showed VWFA and bilateral dorsal-intraparietal activations for words. This further supports the notion that many visual regions in general, even early visual areas, also maintain a predilection for task processing even when the modality is variable and in spite of putative lifelong linguistic cross-modal plasticity.

Furthermore, we find that the VWFA is recruited preferentially for letter and word form, while it was not recruited, and even exhibited deactivation, for an immediately subsequent semantic task suggesting that despite only short sensory substitution experience orthographic task processing can dominate semantic processing in the VWFA. On a wider scope, this implies that at least in some cases cross-modal plasticity which enables the recruitment of areas for new tasks may be dominated by sensory independent task specific activation.

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1. Introduction

The importance of the ability to read – the decoding of symbols aimed at deriving meaning – cannot be overestimated, as it makes it possible to overcome the inherent limitations of the one dimensional linguistic medium (Houston, 2008) while radically modifying existing brain mechanisms (Dehaene et al., 2005, 2010; Price and Devlin, 2003), leading to extensive exploration of the reading process (see reviews in Price (2010) and Hannagan et al.

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.11.009 0028-3932/© 2015 Published by Elsevier Ltd. (2015)). Several foci have been associated with reading letters and words in sighted individuals. The process of word perception begins in the early occipital areas (V1) (Rauschecker, 2011), and then undergoes transformations in the highly studied VWFA (Cohen et al., 2000; Dehaene and Cohen, 2011; Schlaggar and McCandliss, 2007). In addition, a bilateral dorsal intraparietal region has been associated with letter-by-letter reading of words (aka the "serial reading mode"; Cohen et al., 2008).

However, this previous exploration has been almost entirely visual, raising the question of whether the visual modality is necessary and inherently linked to the recruitment of these regions, or whether other modalities could elicit a similar pattern. The brains of congenitally blind individuals offer us a unique

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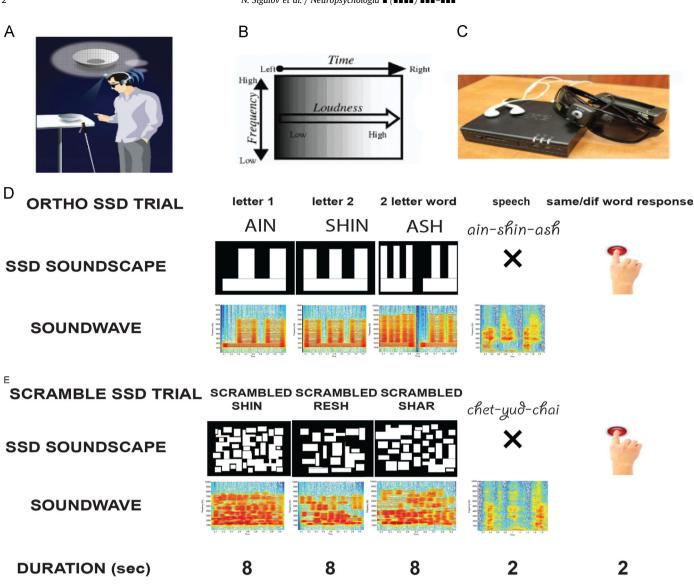


Fig. 1. Experimental Design. (A) Visual-to-auditory sensory substitution was employed to convey visual information to the blind using their intact auditory modality. (B) The transformation algorithm of the vOICe (Meijer, 1992): each image is scanned from left to right, such that time and stereo panning constitute the horizontal axis in its sound representation, tone frequency makes up the vertical axis, and loudness corresponds to pixel brightness. (C) The mobile kit for SSD usage includes a light-weight inexpensive webcam worn on eyeglasses, a computing device (such as a computer or smartphone), and earphones. (D) An example of an OrthoSSD trial: soundscapes of a letter and a soundscape of a word were heard by the subjects, followed by an auditory recording, which was either congruent or incongruent with the soundscapes. (E) An example of a ScrSSD trial: soundscapes of a scrambled letter and a soundscape of a scrambled word were heard by the subjects, followed by an auditory recording,

opportunity to explore how visually-based the process of reading and the recruitment of these areas actually is.

One method of exploring blind reading non-visually is by using Braille, enabling the examination of reading via touch using a special tactile script, and this direction has already seen some fruit (Burton et al., 2002a; Reich et al., 2011; Sadato et al., 1996, 1998). Another possibility is the use of visual-to-audio Sensory Substitution devices (SSDs), non-invasive interfaces which translate information from one sensory modality into another (see methods for elaboration). For example, such devices can convey to the user the full visual shape of the letters and word. To date, the reading network and process of learning to read via SSD has seen only initial exploration focused on the recruitment of the Visual Word Forma Area (VWFA) for reading single letters (Striem-Amit et al., 2012a) and focusing on category selectivity aspects rather than on scrambling or semantic controls. Hence one important question we shall explore here is whether, during the building of entire words from letters through a SSD, the reading network of the CB maintains the same processing foci and hierarchy as the reading network of the sighted.

Another important question is the effect that learning to read via SSD late in life has on the VWFA in the congenitally visuallydeprived brain. On the one hand, the occipital cortex of the blind has been implicated in several key linguistic tasks, including verb generation, verbal memory of single words, speech processing, semantic processing and syntactic processing (Amedi et al., 2003; Bedny et al., 2011; Burton et al., 2002a, 2002b; Cohen et al., 1997; Hamilton et al., 2000; Reich et al., 2011; Roder et al., 2002; Sadato et al., 1996, 1998; Striem-Amit et al., 2012a). Specifically, early occipital areas including V1 and higher-tier areas including VWFA have been implicated in linguistic and verbal memory tasks in the congenitally blind (CB) (Amedi et al., 2003, 2004); Bedny et al. (2011) show extensive visual cortex activation (including in the fusiform) to semantic stimuli in the CB but not in sighted individuals; and Roder et al. (2002) show fusiform activation peaking in a location within the range of coordinates of what is known as the VWFA to overall (semantic and syntactic) linguistic stimuli and activation to semantic stimuli in the fusiform region in the CB.

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