



State-dependent modulation of functional connectivity in early blind individuals

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ABSTRACT

Resting-state functional connectivity (RSFC) studies have provided strong evidences that visual deprivation influences the brain's functional architecture. In particular, reduced RSFC coupling between occipital (visual) and temporal (auditory) regions has been reliably observed in early blind individuals (EB) at rest. In contrast, task-dependent activation studies have repeatedly demonstrated enhanced co-activation and connectivity of occipital and temporal regions during auditory processing in EB. To investigate this apparent discrepancy, the functional coupling between temporal and occipital networks at rest was directly compared to that of an auditory task in both EB and sighted controls (SC). Functional brain clusters shared across groups and cognitive states (rest and auditory task) were defined. In EBs, we observed higher occipito-temporal correlations in activity during the task than at rest. The reverse pattern was observed in SC. We also observed higher temporal variability of occipito-temporal RSFC in EB suggesting that occipital regions in this population may play the role of a multiple demand system. Our study reveals how the connectivity profile of sighted and early blind people is differentially influenced by their cognitive state, bridging the gap between previous task-dependent and RSFC studies. Our results also highlight how inferring group-differences in functional brain architecture solely based on resting-state acquisition has to be considered with caution.

1. Introduction

The study of people deprived of sensory information early in life provides conclusive evidence on how sensory experience shapes the structural and functional architecture of the brain (Frasnelli et al., 2011). Recent researches involving early blind individuals have shed new lights on the old 'nature versus nurture' debate regarding brain development: whereas the recruitment of occipital regions by non-visual inputs in the congenitally blind highlights its dependence upon experience to organize itself (nurture's influence), the observation of specialized cognitive modules in the occipital cortex of congenitally blind, similar to those observed in the sighted, highlights the intrinsic constraints imposed to such plasticity (nature's influence) (Collignon et al., 2011; Dormal and Collignon, 2011; Reich et al., 2012; Ricciardi et al., 2014).

Gaining deeper insights into how occipital regions in early blind individuals (EBs) are organized to support sensorimotor and cognitive functions not only requires studying their response properties (functional specialization), but also understanding how they are integrated into brain networks (functional integration) (Friston, 2003). An increasingly popular approach to study short and long-range brain interactions is to measure functional connectivity (FC) during resting-state (RS; van den Heuvel and Hulshoff Pol, 2010). With resting-state functional connectivity (RSFC), spontaneous fluctuations in functional magnetic resonance imaging (fMRI) signal, observed while participants are resting, are correlated to infer FC between intrinsically connected brain regions (Biswal et al., 1995). Therefore, RSFC is a measure of temporal synchrony of fMRI signal between distinct brain regions. Since functional networks have distinct temporal characteristics,

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separate functional networks can be identified from a single time series of resting fMRI data (Beckmann et al., 2005).

Research on the effect of early visual deprivations using RSFC protocols has evidenced both enhanced segregation (i.e. decreased connectivity) and integration (i.e. increased connectivity) of occipital regions (see Bock and Fine, 2014 for review). A striking and often replicated result emerging from those studies is the reduced connectivity of EBs' occipital regions with primary somatosensory and auditory areas (Bedny et al., 2011; Burton et al., 2014; Liu et al., 2007; Yu et al., 2008; Striem–Amit et al., 2015). This reliable effect at rest contrasts with the large amount of studies reporting enhanced task-dependent activations of occipital regions during the processing of auditory and tactile inputs in EBs (see Bavelier and Neville, 2002; Frasnelli et al., 2011 for review). Importantly, the functional relevance of occipital activity to EB's non-visual sensory/perceptual processing is supported by studies showing reduced performance to specific tactile and auditory tasks following the disruption of EB's occipital cortex through the application of transcranial magnetic stimulation (TMS) (Cohen et al., 1997; Collignon et al., 2007, 2009). Moreover, TMS directly applied over the occipital cortex can elicit paresthesiae in the fingers of early blind braille readers (Cohen et al., 1997; Ptito et al., 2008). Further support comes from studies of effective connectivity (causal connectivity; Friston, 1994) estimated by dynamic causal modelling of fMRI data (Friston, 2003) or by combining TMS with Positron Emission Tomography (PET) (measuring activity induced by magnetically exciting distant cortical regions), which have shown stronger coupling between auditory or somatosensory areas and occipital regions in EBs than in SCs (fMRI: Collignon et al., 2013; Klinge et al., 2010, PET and TMS: Wittenberg et al., 2004). Finally, the participation of occipital cortex in non-visual processes early in time following stimuli presentation (Collignon et al., 2009; Leclerc et al., 2000; Röder et al., 1999) implies the existence of direct links between occipital and other non-visual sensory regions.

We suggest that this apparent inconsistency between RSFC and task-dependent studies originates from the presupposition that RS networks are good proxies for networks instantiated during cognitive/perceptual processing (Andric and Hasson, 2015). Even though group level RSFC patterns have been documented to be similar to task co-activation patterns (Cordes et al., 2000; Smith et al., 2009; Wig et al., 2014), recent work has shown that whole-brain FC networks can be fundamentally reshaped by experience (e.g. Gordon et al., 2014; Orban et al., 2015; Lewis et al., 2009; Tambini et al., 2010), and over short periods of time (Allen et al., 2012; Hutchison et al., 2013b); that they are not constrained by RS topologies, and that this holds particularly true for the connectivity structure of sensory systems (e.g. Andric and Hasson, 2015; Mennes et al., 2013). Importantly, investigations of the effect of task-focused attention versus rest/mind wandering in sighted individuals have shown functional coupling across brain regions to be state-dependent (Hampson et al., 2002, 2004; Jiang et al., 2004; Newton et al., 2007). Specifically, functionally relevant connections show increased connectivity whereas irrelevant connections are decreased during task as compared to rest (Bartels and Zeki, 2005; Nir et al., 2006), with the resulting patterns of FC being specific enough to reliably predict participants' cognitive states (Shirer et al., 2012). Furthermore, evidence that differences in FC pattern between populations can be task-dependent (Çetin et al., 2014; Nair et al., 2014) compellingly illustrates how inferring differences in functional integration between groups solely based on RSFC should be subject to caution.

What is RSFC representative of then? The current view is that the wandering mind sequentially explores multiple functional modes, each with a unique pattern of connectivity, and sustaining a different function (Deco et al., 2011; Karahanoglu et al., 2013). Consequently, a connection's strength will vary as a function of time (see Hutchison et al., 2013a, 2013b), with more temporally variable connections being members of a larger set of modes (Allen et al., 2012). A secondary consequence of this dynamic nature is that connections measured over

a whole run will be representative of no single functional mode, but of their average (Hutchison et al., 2013b, Smith et al., 2012). Of note, if a mode were to be less prevalent in a group, or in competition with a greater number of modes, its connectivity pattern would be more strongly diluted when computed over a whole run, and may consequently appear weaker.

Therefore, the goal of the current study was twofold. First, to investigate how cognitive states, rest and an auditory sensory/perceptual task, would impact FC between occipital and temporal cortices in both EBs and SCs. Second, to verify whether difference in RSFC between EBs and SCs might be caused by higher variance in the connectivity profile of occipito-temporal connections. To investigate the topic of cognitive state, an auditory task was chosen because temporo-occipital RSFC has been reliably demonstrated to be lower in EBs than in SCs (Bedny et al., 2011; Burton et al., 2014; Liu et al., 2007; Striem–Amit et al., 2015; Yu et al., 2008), and because auditory processing elicits strong responses in both the occipital and temporal cortices of EBs (Collignon et al., 2011, 2013; Dormal et al., 2016). Thus, participants underwent two fMRI runs, a RS one, and one where they were involved in a challenging auditory task (Collignon et al., 2011). FC was extracted for each run and population, then the presence of an interaction between cognitive state and groups was tested. Additionally, for the RS run, a connection's variability was measured as a function of time and the resulting metrics compared across groups. Biases caused by a priori definition of regions of interest (Zalesky et al., 2010; Park et al., 2013) were avoided by grouping voxels into functionally homogeneous regions. The actual method used, Bootstrap Analysis of Stable Clusters (Bellec et al., 2010), has recently been shown to perform well compared to other methods when it comes to subdividing the brain into meaningful functional regions (Ryali et al., 2015).

Based on studies revealing an increase in FC between functionally related areas and a decrease between functionally unrelated areas during tasks (Bartels and Zeki, 2005; Nir et al., 2006), our hypothesis was that the FC between auditory and occipital regions would be differently modulated by the cognitive states in EBs and SCs. Additionally, if some of EBs' occipital regions do participate in a greater number of modes, their specific connections with auditory areas should be more variable than in SCs.

2. Materials and methods

2.1. Participants

The data of fourteen EBs [4 females, age range 27–61 (mean \pm SD, 42 ± 11) and 16 SCs [7 females, age range 23–60 (mean \pm SD, 39 ± 14) were included in the analyses (see Supplementary Table 1 for more information on blind participants). Student's *t*-test did not reveal any statistical age differences between groups. One additional SC participated in the study but was excluded from the analyses due to excessive motion during scanning acquisition (see below). Both groups were blindfolded throughout the fMRI acquisition. None of the EBs had ever had functional vision allowing pattern recognition or visually guided behaviour. At the moment of testing, all EBs were totally blind except for two who had only rudimentary sensitivity for brightness with no pattern vision. In all cases, blindness was attributed to peripheral deficits with no neurological impairment. For all subjects, pure-tone detection thresholds at octave frequencies ranging from 250 to 8,000 kHz were within normal limits in both ears. All of the procedures were approved by the research ethic and scientific boards of the Centre for Interdisciplinary Research in Rehabilitation of Greater Montreal and the Quebec Bio-Imaging Network. Experiments were undertaken with the understanding and written consent of each subject.

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