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Early visual deprivation changes cortical anatomical covariance in dorsal-stream structures

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ABSTRACT

Early blind individuals possess thicker occipital cortex compared to sighted ones. Occipital cortical thickness is also predictive of performance on several auditory discrimination tasks in the blind, which suggests that it can serve as a neuroanatomical marker of auditory behavioural abilities. In light of this atypical relationship between occipital thickness and auditory function, we sought to investigate here the covariation of occipital cortical morphology in occipital areas with that of all other areas across the cortical surface, to assess whether the anatomical covariance with the occipital cortex differs between early blind and sighted individuals. We observed a reduction in anatomical covariance between the right occipital cortex and several areas of the visual dorsal stream in a group of early blind individuals relative to sighted controls. In a separate analysis, we show that the performance of the early blind in a transposed melody discrimination task was strongly predicted by the strength of the cortical covariance between the occipital cortex and intraparietal sulcus, a region for which cortical thickness in the sighted was previously shown to predict performance in the same task. These findings therefore constitute the first evidence linking altered anatomical covariance to early sensory deprivation. Moreover, since covariation of cortical morphology could potentially be related to anatomical connectivity or driven by experience-dependent plasticity, it could consequently help guide future functional connectivity and diffusion tractography studies.

Introduction

The scientific literature is quite rich with research documenting the striking crossmodal plasticity that takes place in the brain of congenitally and early blind (EB) individuals (see Voss et al., 2010; Merabet and Pascual-Leone, 2010 for reviews), where deafferented visual brain areas are recruited to carry out non-visual processing. More recently, several groups have started investigating the potential neuroanatomical markers of crossmodal plasticity in the blind as there is ample evidence that experience can shape structural features within the normal brain (see Zatorre et al., 2012). One important neuroplastic change observed in early and congenitally blind individuals relates to increased occipital cortical thickness (CT) relative to sighted controls (Park et al., 2009; Jiang et al., 2009; Bridge et al., 2009; Anurova et al., 2014). Importantly, it has been shown that occipital CT is strongly predictive of auditory abilities in the blind (Voss and Zatorre, 2012), thus confirming that these neuroanatomical changes are behaviourally relevant, and likely result from some form of adaptive compensatory plasticity. However, it remains unknown whether these changes in cortical structure reflect only local alterations or may also reflect network-level modulations.

Neuroanatomical measurements have been proposed as means to characterize brain connectivity through covariation analyses (Bullmore et al., 1998; Mechelli et al., 2005; Lerch et al., 2006). Indeed, brain areas that are highly correlated in size are often part of systems that are known to subserve particular behavioural or cognitive functions (see Alexander-Bloch et al., 2013). For instance, posterior (Wernicke) and anterior language (Broca) areas co-vary strongly in the cortical thickness (Lerch et al., 2006). Similarly, the grey matter volume of the hippocampus co-varies most strongly with other regions known to be part of the memory system (Bohbot et al., 2007). CT in particular has been proposed as a valid measure of cortical covariation since previous morphometric correlations of cortical thickness data have successfully produced structural networks of covariance that resemble tract-tracing data (Mitelman et al., 2005; Lerch et al., 2006; Bernhardt et al., 2008; Gong et al., 2012), while animal tracer studies have additionally shown that cortical thickness can predict anatomical connectivity (Barbas, 1986; Barbas and Rempel-Clower, 1997; Dombrowski et al., 2001).

Here, in light of the above findings, we sought to investigate the covariation (i.e. anatomical covariance) of occipital cortical morphology with that of all other points (i.e. vertices (see methods)) across the cortical surface, following the method proposed by Lerch et al. (2006),

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in order to assess how early visual deprivation may alter the corticocortical connectivity patterns. We used a seed-based approach to carry out the covariation analyses. The choice of an occipital seed was based on our previous findings relating auditory behaviour to occipital CT (Voss and Zatorre, 2012). We hypothesized that the seed region (located in the right cuneus) in the EB might show reduced covariance with other non-occipital visual areas, now deafferented from their usual input, whereas enhanced covariance with other primary sensory areas might be observed given the abundant crossmodal recruitment observed in the occipital cortex of the EB.

Furthermore, previous work has shown that examining anatomical covariance can be an effective way to characterize individual differences. For instance, Lee et al. (2013) showed that greater anatomical covariance between several linguistically relevant areas was associated with better vocabulary abilities in a sample of developing children. Similarly, here we asked whether better auditory abilities in the EB, could be linked to greater cross-cortical covariance between the seed region and task-relevant brain areas. Finally, although the primary goal here was to investigate the effects of early visual deprivation specifically, we also present some data obtained from late-onset blind (LB) individuals. This was done to assess whether an onset of blindness occurring after the visual system had fully developed with proper input would lead to differential patterns of covariance compared to early blindness.

Methods

Subjects

Data from fourteen early-blind (EB) individuals (38.2 ± 13.8 years (y) of age; 10 males and 4 females), thirteen late-blind (LB) (46.6 ± 8.5 y; 5 males and 8 females), and nineteen sighted subjects (37.6 ± 12.0 y; 8 males and 11 females) were included in the study. EB individuals all lost their sight no later than the age of 4 (average age of blindness onset was of 0.5 ± 1.2 y and average duration of blindness was of 37.7 ± 14.3 y), whereas the LB all lost their sight after the age of 7 (average age of blindness onset was of 29.4 ± 15.4 y and average duration of blindness was of 17.5 ± 10.6 y). Complete demographic data and causes of blindness are displayed in Table 1. All subjects gave written informed consent in accordance with the guidelines approved by the Montreal Neurological Institute and the Nazareth and Louis-Braille Institute (NLBI) for the blind. The research protocols were approved by the ethics committees of the *Centre de Recherche Interdisciplinaire en Réadaptation* (CRIR), which coordinate research with blind subjects sponsored by the Nazareth and Louis-Braille Institute (NLBI) for the blind, and by the research ethics board of the Montreal Neurological Institute, where the scanning procedures were carried out.

Table 1
The 'onset' column refers to the age at which the subjects lost their sight. The 'duration' column refers to the number of years that the subjects have been blind. The 'LP' column indicates whether subjects still had any residual light perception.

Subject demographic information						
Subjects	Age	Gender	Onset	Duration	LP	Cause of blindness
EB1	32	F	4	28	No	Retinoblastoma
EB2	27	F	0	27	No	Retinal detachment
EB3	37	M	0	37	No	Congenital glaucoma
EB4	57	F	0	57	No	Retinopathy of prematurity
EB5	21	M	0	21	No	Retinopathy of prematurity
EB6	26	M	1	26	No	Congenital cataracts
EB7	40	M	0	40	No	Retinopathy of prematurity
EB8	52	M	0	52	No	Medical accident (retina damage)
EB9	20	M	0	20	Yes	Congenital malformation (no cristallin)
EB10	59	M	0	59	Yes	Congenital cataracts
EB11	24	M	2	21	no	Retinoblastoma
EB12	45	M	0	45	no	Congenital glaucoma
EB13	39	M	0	39	Yes	Retinopathy of prematurity
EB14	56	F	0	56	Yes	Retinal detachment
LB1	44	M	21	23	No	Congenital glaucoma
LB2	48	F	28	20	No	Diabetic retinopathy
LB3	48	F	24	24	No	Ischemic retinopathy
LB4	53	F	30	23	Yes	Retinal degeneration
LB5	53	F	19	34	No	Glaucoma
LB6	60	F	48	12	No	Failed cornea transplant
LB7	52	M	50	2	Yes	Dehydration of the optic nerve
LB8	59	F	54	5	No	Retinitis pigmentosa
LB9	46	F	43	3	Yes	Glaucoma + retinal detachment
LB10	48	M	32	16	Yes	Retinal detachment
LB11	29	F	17	13	Yes	Congenital Glaucoma
LB12	37	M	9	18	No	Congenital Glaucoma
LB13	42	M	7	35	No	Lenticular fibroplasia

Behavioural tasks

The behavioural data used in the current study are taken from two auditory tasks that are described in greater detail elsewhere (see Voss and Zatorre, 2012). The first, a pitch discrimination task, required subjects to specify which of the two sequentially presented tones was higher in pitch. The reference tone was a 500 Hz pure tone and the task followed a 2-down/1-up staircase procedure, which produces runs of increasing and decreasing the difference between stimuli whose endpoints (reversal points) bracket the 71% threshold (Levitt, 1970). One staircase run was completed after 15 reversals and the geometric mean of the value of the last 8 reversals was taken as the threshold. The threshold is therefore unaffected by the choice of starting difference, because the first seven endpoints are not entered into the calculation. Four separate runs were conducted for each subject and averaged to produce the final value (i.e. the individual thresholds). The second task, first described by Foster and Zatorre (2010b), was a transposed-melody discrimination task. Here, subjects were required to determine whether two sequential melodies (unfamiliar melodies in the Western major scale) were identical or different. The difficulty of this task lies in the fact that the all the notes of the second stimulus pattern were transposed 4 semitones higher in pitch (in both the "same" and "different" trials). In "different" trials, one note was altered by 1 semitone to a pitch outside the pattern's new key, maintaining the melodic contour. This task therefore requires that the listener compares the pattern of pitch intervals (frequency ratios) between each successive tone, and as such requires a more abstract, relational type of processing.

Image acquisition and cortical thickness measurements

T1-weighted magnetization-prepared rapid gradient-echo images (time echo = 2.98 ms, time repetition = 2300 ms, matrix size: 256 × 256, FOV = 256 mm, slice thickness = 1 mm, flip angle = 9°, voxel size 1 mm^3) were acquired on a Siemens 3 T MRI scanner. All T1 images were then submitted to the CIVET pipeline (version 1.1.9; Ad-Dab'bagh et al., 2006; Zijdenbos et al., 2002). T1 images were registered to the ICBM152 nonlinear sixth generation template with a 12-parameter linear transformation (Collins et al., 1994), RF inhomogeneity-corrected (Sled et al., 1998) and tissue-classified (Tohka et al., 2004; Zijdenbos et al., 1998). Deformable models were then used to create the white/grey matter and grey matter/cerebrospinal fluid interfaces for each hemisphere separately (MacDonald et al., 2000; Kim et al., 2005), resulting in four polygonal mesh surfaces of 40,962 vertices each. Both surfaces were non-linearly aligned to a surface template (Lyttelton et al., 2007) using a 2D registration procedure that improves the anatomical correspondence of vertices in all subjects (Robbins, 2004). From these surfaces, the *t*-Laplace metric was derived by using the Laplacian method for determining the distance between the white and grey surfaces (Haidar and Soul, 2006; Lerch and Evans, 2005). The thickness data were subsequently blurred using a 20-mm surface-based diffusion blurring kernel in preparation for statistical