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White matter connectivity between occipital and temporal regions involved in face and voice processing in hearing and early deaf individuals

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Neuroplasticity following sensory deprivation has long inspired neuroscience research in the quest of understanding how sensory experience and genetics interact in developing the brain functional and structural architecture. Many studies have shown that sensory deprivation can lead to cross-modal functional recruitment of sensory deprived cortices. Little is known however about how structural reorganization may support these functional changes. In this study, we examined early deaf, hearing signer and hearing non-signer individuals using diffusion MRI to evaluate the potential structural connectivity linked to the functional recruitment of the temporal voice area by face stimuli in deaf individuals. More specifically, we characterized the structural connectivity between occipital, fusiform and temporal regions typically supporting voice- and face-selective processing. Despite the extensive functional reorganization for face processing in the temporal cortex of the deaf, macroscopic properties of these connections did not differ across groups. However, both occipito- and fusiform-temporal connections showed significant microstructural changes between groups (fractional anisotropy reduction, radial diffusivity increase). We propose that the reorganization of temporal regions after early auditory deprivation builds on intrinsic and mainly preserved anatomical connectivity between functionally specific temporal and occipital regions.

1. Introduction

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Decades of neuroscientific research have revealed the extraordinary capacity of the human brain to adapt in response to experience and lack of specific sensory inputs (Pascual-Leone et al., 2005). After sensory deprivation, such as blindness or deafness, the sensory deprived cortices can reorganize and process information from the spared sensory modalities (Bavelier and Neville, 2002; Heimler et al., 2014). In the case of deafness, for instance, temporal auditory regions can be functionally recruited to respond to visual (Finney et al., 2001; Fine et al., 2005) and tactile (Auer et al., 2007; Karns et al., 2012) inputs.

It has been suggested that cross-modal reorganization following early sensory deprivation reflects the functional specialization of the colonized cortical regions (Dormal and Collignon, 2011; Reich et al., 2011; Ricciardi et al., 2014). For instance, Lomber and colleagues have reported that, in deaf cats, superior visual motion detection is selectively impaired if a specific region in the dorsal auditory cortex, which processes auditory motion in hearing cats, is transiently suppressed (Lomber et al., 2010). In deaf humans, supporting evidence has recently been provided by a study showing rhythm-specific visual activations in posterior-lateral and associative auditory regions (Bola et al., 2017) and, further, by our observation of preferential responses to faces and face discrimination in the human temporal voice sensitive area (TVA) as a consequence of early auditory deprivation (Benetti et al., 2017).

How does specific non-auditory information reach the reorganized temporal cortex of deaf individuals? Evidence that cross-modal remapping of temporal regions is associated with reorganization of long-range functional interactions between auditory and visual cortices has been

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Abbreviations: STG, Superior Temporal Gyrus; STS, Superior Temporal Sulcus; pSTS, Posterior superior Temporal Sulcus; FFA, Face-fusiform Area; V2/3, Boundary between Extrastriate V2 and V3 Areas; TVA, Temporal Voice-sensitive Area.

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reported for visual motion detection in deafness (Shiell et al., 2014). Further, in our previous study we reported that face-selective cross-modal activation in the deaf TVA is primarily modulated by increased feed-forward effective connectivity from extrastriate visual regions (V2/3) in early deaf humans (Benetti et al., 2017). This observation confirms previous findings reported in early blind individuals (Collignon et al., 2013) and suggests that the reorganization of long-range functional connectivity between sensory cortices might play a key role in functionally selective cross-modal plasticity.

Despite the growing evidence of selective neurofunctional plasticity in both blindness and deafness, whether these changes relate to alterations of white matter structural connections still remains controversial. In particular, the observation of increased functional connectivity within reorganized networks (e.g. between temporal and occipital regions) seems not to be systematically paralleled by consistent observations in structural connectivity, where both reductions and increases have been observed in blind (Shu et al., 2009; Lao et al., 2015; Bauer et al., 2017) and deaf (Lyness et al., 2014; Karns et al., 2017) individuals. This inconsistency might be due to the fact that previous studies have mostly focused on functional and structural connectivity separately.

Reorganization of the face-voice human system in early deafness represents a unique opportunity to specifically address the relationship between changes in local cortical responses and long-range functional and structural connectivity within a functionally defined network. In fact, there is evidence of direct connections between the fusiform faceselective area (FFA) and the mid-anterior portion of the superior temporal gyrus (STG) responding selectively to human voices in the right hemisphere of hearing individuals, (i.e. TVA; Blank et al., 2011) as well as direct connections between extrastriate visual and temporal auditory regions in humans (Beer et al., 2011).

In this study, we follow-up on our previous observation (Benetti et al., 2017) by applying a hypothesis-driven approach to the examination of white matter connectivity in the same deaf individuals showing face-selective reorganization of both temporal regions and long-range occipito-temporal functional coupling.

2. Materials and methods

2.1. Participants

Forty-four participants were included in this study. Fourteen were early deaf (ED; 13 since birth and one before age 4; mean age 32.79 ± 7.21 ; 7 males), 15 were hearing controls fluent in the use of the Italian Sign Language (HC-SL; mean age 34.07 ± 5.97 ; 5 males)

and 15 were hearing controls (HC; mean age 30.40 ± 5.09 ; 8 males). All the participants participated also in our study on face-selective cross-modal plasticity in the temporal voice area (Benetti et al., 2017). ED participants presented with severe to profound congenital deafness in both ears with the exception of one participant who developed deafness before the age of 4 years. A group of hearing sign language (Lingua Italiana dei Segni; LIS) users was included to control for the potential confound of visual language use; the age of acquisition and the exposure to LIS use was comparable between the ED and HC-SL groups (see Table 1). All participants were currently healthy, had no medical history of neurological or psychiatric disorders and were no under psychoactive medication. They were tested on non-verbal IQ, hand preference and composite measures of face recognition (a detailed description of these tests has been provided in Benetti et al., 2017). There were no differences for age, non-verbal IQ scores and hand preferences between groups while both the ED and HC-SL outperformed the HC group on face recognition (Table 1). The study was approved by the Committee for Research Ethics of the University of Trento; all participants gave informed consent in agreement with the ethical principles for medical research involving human subject (Declaration of Helsinki, World Medical Association) and the Italian Law on individual privacy (D.l. 196/2003).

2.2. Image acquisition

Four imaging datasets were acquired for completion of this study: a functional MRI face localizer, a functional MRI voice localizer, diffusionweighted MR images and structural T1-weighted images. Data acquisition was carried out at the Center for Mind/Brain Science of the University of Trento, using a Bruker BioSpin MedSpec 4T MR-scanner.

Functional MRI sequence and experiment. A detailed description of the experimental procedure and stimuli for the face and voice localizers have been provided elsewhere (Benetti et al., 2017). In brief, the same gradient-echo planar imaging (EPI) sequences with continuous slice acquisition (TR = 2.200 ms, TE = 33 ms, slices = 37, slice thickness = 3 mm, Slice gap = 0.6 mm, image matrix = 64×64) was applied and a total of 274 and 335 vol were acquired for the face and voice localizer respectively. The voice localizer was acquired in the HC group only during a 12 min task in which neutral human vocal sound ("A"), scrambled human vocal (random mix of magnitude and phase of each Fourier component but same global energy and envelope of neutral vocal stimuli) and object sounds were presented in a block-design manner (10 blocks for each category). The face localizer also consisted of a block-design task in which images of human faces (static and neutral)

Table 1

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Demographics, behavioral performances and Italian Sign Language aspects of the 44 subjects participating in the diffusion and functional MRI experiment.
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Demographics/Cognition	Participants in Diffusion/Functional MRI Experiment			
	Hearing Non-Signers (n = 15)	Hearing Signers (n = 14)	Early Deaf (n = 14)	Statistics
Mean Age, y(SD)	30.40 (5.09)	34.07(5.97)	32.79(7.21)	F-test = 1.382
				P-value = 0.263
Gender, male/female	8/7	5/10	7/7	$X^2 = 1.381$
				P-value = 0.501
Hand Preference, % (right/left ratio)	71.36(48.12)	61.88(50.82)	58.63(52.09)	K-W test = 1.15
				P-value = 0.564
Non-verbal IQ, Mean estimate (SD)	123.4(8.38)	124.80(5.61)	120.23(9.71)	F-test = 1.073
				P-value = 0.352
Composite Face Recognition, z-scores (SD)	-0.124(1.45)**	1.547(1.43)	1.634(1.74)	F-test = 5.751
				P -value = 0.006
LIS Exposure, y(SD)	-	25.03(13.85)	21.08(10.25)	t-test = -0.823
				P-value = 0.418
LIS Acquisition, y(SD)	-	11.38(9)	9.033(11.91)	M-W.U test = 112
				P-value = 0.505
LIS Frequency, Percent time/y (SD)	-	68.59(44.88)	84.80(26.09)	M-W. U test = 87.5
				<i>P</i> -value = 0.364

(**) main effect of group (P < 0.006), ED versus HC (p < 0.016), HS-SL versus HC (p < 0.016). K-W, Kruskal-Wallis; M – W, Mann-Whitney; y, years; SD, Standard Deviation.

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