

Functional and structural brain connectivity in congenital deafness

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Research Article

Keywords: Deafness, fMRI, DTI, Brain Connectivity, Sign Language

Posted Date: March 1st, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-246296/v1>

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Version of Record: A version of this preprint was published at Brain Structure and Function on March 19th, 2021. See the published version at <https://doi.org/10.1007/s00429-021-02243-6>.

Abstract

Several studies have been carried out to verify neural plasticity and the language process in deaf individuals. However, further investigations regarding the intrinsic brain organization on functional and structural neural networks derived from congenital deafness is still an open question. The objective of this study was to investigate the main differences in brain organization manifested in deaf individuals, concerning the resting-state functional patterns, and white matter structuring. Functional and diffusion-tensor magnetic resonance imaging modalities were acquired from 18 congenitally deaf individuals and 18 age-sex-matched hearing controls. Compared to the hearing group, the deaf individuals presented higher functional connectivity (FC) among the posterior cingulate cortex node of the default mode network (DMN) with visual and motor networks, lower FC between salience networks, language networks, and prominence of functional connectivity changes in the right hemisphere, mostly in the frontoparietal and temporal lobes. In terms of structural connectivity (SC), we found changes mainly in the occipital and parietal lobes, involving both classical sign language support regions as well as concentrated networks for focus activity, attention, and cognitive filtering. Our findings elucidate the general brain network modifications, contributing to a better understanding of brain plasticity driven by deafness.

Introduction

Hearing is one of the essential parts of human communication, offering the possibility to differentiate speech sounds. Hearing impairment has a significant impact on the individual's life quality, mainly due to complications related to communication in the social environment (Dobie and Van Hemel 2005). According to the World Health Organization (WHO), in 2004, there were 276 million people worldwide with hearing loss (World Health Organization 2008), and, in Brazil, 14,5% of the population presented some degree of hearing loss according to 2000 demographic census (IBGE 2002). Changes in the auditory system can occur at any stage of life, and their study and treatment, when possible, are of great importance.

It is evidenced that hearing loss impairs oral language development, especially if the auditory deficit is congenital or occurs in the pre-lingual period (Sobreira et al. 2015). One consequence is the inability to develop oral language in a natural way (Mayberry et al. 2002), which can become a social obstacle and lead to social isolation (Miller et al. 1994). Fortunately, language difficulties found in deaf children are completely preventable, since the major cause of social isolation is the lack of early exposure to a language form accessible to their natural abilities (Mayberry et al., 2002). It is well-known that deaf children require a rich and fruitful linguist environment that is adaptable to their sensorial capabilities, mainly in the early years of life (Petitto 1994; Petitto et al. 2000; Mayberry et al. 2002; Neville and Bavelier 2002; Schick et al. 2010). Therefore, early diagnosis is one of the decisive factors, since the neurological maturation responsible for the cognitive development associated with language occurs in childhood (Gazzaniga 2000).

Sign language can be naturally developed in deaf individuals if their visual and manual capabilities are preserved. However, oral and sign languages use different sensory modalities because motor control of the tongue and hands activate different neural substrates in the brain. Comparative analysis of such forms provides us with valuable information about the specificity of the neural architecture responsible for the acquisition and interpretation of language in humans (Petitto 1994). Neuroimaging studies have reported activation in classical language-related brain regions, Wernicke's and Broca's areas, in deaf individuals (Neville et al. 1998; Petitto et al. 2000; Mayberry et al. 2002; MacSweeney et al. 2008). In addition, Bavelier et al. (2001) also observed specific changes in the organization of brain areas related to the motor cortex in congenital deafness with early exposure to sign language. Sacks (1990) observed that some auditory regions of the brain are reallocated for visual use in deaf children who communicate by sign language, thus strengthening the idea of brain adaptation due to hearing deprivation.

In addition to the isolated brain regions differences evidenced by the previous studies, there are also interesting findings related to the brain organization level. Increased brain functional connectivity between the limbic system and regions involved in visual and language processing was observed (Wenjing et al., 2015), suggesting reinforcement of visual and verbal information processing in deaf prelingual adolescents. On the other hand, decreased brain functional connectivity was detected by the same authors between the visual and language brain regions possibly due to diminished reading or speaking skills in deaf individuals. Furthermore, it was observed a brain morphological network alteration in prelingual deaf adults compared to normal controls, but not in post-lingual deaf adults, indicating that auditory experience could affect the morphology of brain networks in deaf adults (Kim et al, 2014). Wolak et al. (2019) also relate that even a partial hearing deficit, as noticed in congenital sloping loss, can affect the brain functional organization, pointing to the role of sensitive periods in brain development.

Despite all the contributions provided by such studies, questions are still open considering the impact of the absence of hearing *stimuli* in the brain. For example, better knowledge about the pattern of cortical activity at rest, as well as the overall configuration of white matter tracts (MacSweeney et al. 2008). In summary, the literature has elucidated alteration on the brain white matter density on the Heschl gyrus (BA 41,42,43), thicker cerebellum cortex (BA 44), gray matter density preserved in the primary auditory cortex, increased functional connectivity in prelingual deafness (Kim et al, 2014), and abnormal functional connectivity and cortical reorganization in the brain at rest in adults that lost hearing by ototoxic drugs (Zhengliang et al, 2015).

Hence, according to the findings reported in previous studies regarding the punctual differences in brain regions, we assumed that alteration of brain functional and structural networks could also be evident, especially on the Default Mode Network (DMN) due to the impact of such neuronal organization on several cognitive processes. Current advances in brain imaging techniques and computational methods provide support for such new findings, necessary for a better understanding of the cerebral adaptive process, in the case of hearing deprivation. Therefore, based on the findings enlightened by the localized brain functional and structural alterations, there is a hypothesis that the larger brain organization

goal is to contribute to elucidating the main brain adaptations in DMN functional and structural networks present in deaf individuals, by using multimodal magnetic resonance imaging (MRI).

Materials And Methods

Participants

The research volunteers were selected from a group of patients that routinely makes a medical and audiological evaluation in order to certify the individual health status. It included eighteen subjects with congenital deafness (8 men, 10 women, with age ranging from 18 to 45 years old), profound sensorineural hearing loss in both ears with deafness diagnosed ranging from 8 months to 1.5 years. 1 individual was deaf through maternal rubella, 3 reported genetics as their cause of deafness, and 14 had an unknown cause of deafness. All the participants used sign language as their first language, which was learned at the age ranging from 9 months to 2 years old, and none of them used hearing aids. The medical assessments were analyzed and ensured the absence of any neuropsychological or neurological comorbidities.

A control group of hearing participants, paired in sex and age, was also considered (8 men, 10 women, with age ranging from 18 to 45 years old). The data from the control group was acquired retrospectively, using the research database of the Center of Image Science and Medical Physics (CCIFM), at the HCFMRP. Therefore, the hearing individuals did not perform the audiometric evaluation. It was assumed they had auditory thresholds within the normal range since they participated in other functional MRI studies as a control group (Siva Costa et al. 2019, Pessini et al. 2018, Rondinoni et al. 2013).

The Research Ethics Committee of the Medical School of Ribeirao Preto approved the study. A sign language interpreter was present to assist the deaf individuals in any doubts related to the study and brain images acquisition. After being informed and agreeing with the terms of the study, all participants signed the Free and Clarified Consent Form.

Pure-tone audiometry test

We used the AD 28 audiometer equipment (Interacoustics manufacturer). All deaf participants underwent tonal threshold audiometry by air in the frequencies of 250 Hz, 500 Hz, 1000 Hz, 2000 Hz, 3000 Hz, 4000 Hz, 6000 Hz, and 8000 Hz, with pure tone, using earphones, in an acoustic cabin, which is inside a room also acoustically treated, under appropriate conditions of temperature, humidity, and luminosity. Bone tonal threshold audiometry was performed at frequencies of 500 Hz, 1000 Hz, 2000 Hz, 3000 Hz, 4000 Hz whenever airway thresholds were greater than 25 dB NA. The pure tone signal was presented by a bone vibrator (attached to an arch) positioned in the mastoid.

Image acquisition

MRI images were performed using a 3T system (Philips Achieva, The Netherlands), adapted with a full-channel head coil for signal reception, available at HCFMRP.

Three imaging modalities were used: functional magnetic resonance imaging (fMRI), diffusion tensor imaging (DTI), and T1-weighted (T1W) structural imaging. fMRI was performed with 2D EPI readout and the following parameters: TR/TE = 2000/30 ms, FOV = 240 × 240 mm², in-plane voxel size = 1.83 × 1.83 mm, 29 axial slices, slice thickness = 4 mm, time per slice = 66 ms, 200 volumes. DTI was performed with 32 gradient directions, b-factor = 1000 mm/s², $b_0 = 0\text{ mm/s}^2$, TR/TE = 8391/65 ms, FOV = 256 × 256 mm², matrix = 128 × 128, 72 axial images of 2-mm thickness, resulting in an isotropic spatial resolution of 2.0 × 2.0 × 2.0 mm³. For anatomical reference, T1W images were acquired using a 3D gradient-echo sequence with the following parameters: TR/TE = 9.7/4 ms, flip angle = 12°, FOV = 256 × 256 mm², matrix = 256 × 256, slice thickness = 1 mm. The total scan time for a subject was approximately 25 minutes.

Image processing

DTI and fMRI data were processed and analyzed using FSL (Oxford Center for Functional MRI of the Brain, Oxford University) (Jenkinson et al. 2012) and Connectivity Toolbox (CONN) (Whitfield-Gabrieli and Nieto-Castanon 2012), which is part of the SPM toolkit (Statistical Parametric Mapping, University College London) (Friston et al. 1994). Results were visualized in 3D Slicer software (Surgical Planning Laboratory, Harvard University) (Pieper et al. 2006). Detailed procedures are described as follows:

fMRI preprocessing

includes image reorientation using the anterior commissure as a reference point for the origin; slice time correction; realignment of functional images; registration between functional and anatomical images; segmentation of anatomical images; normalization for MNI space (Collins et al. 1994); and spatial smoothing of functional images (Gaussian filter, FWHM = 6 mm). Functional connectivity (FC) based on regions of interest (ROI) was performed in CONN using its functional atlas with 32 regions (Whitfield-Gabrieli and Nieto-Castanon, 2012). First, unwanted fluctuations in the fMRI signal were removed using the six parameters of motion correction residual and their first-time derivatives, and global signal of white and gray matters as regressors. For the ROI-to-ROI analysis, a correlation matrix was obtained from the bivariate correlation between the time series of each ROI. Additionally, we performed the Independent Component Analysis (ICA). The implementation consists of temporal concatenation across multiple subjects followed by a group-level dimensionality reduction using Principal Component Analysis, and FastICA to obtain spatially-independent components (IC). The back-projection used dual regression with a univariate spatial-regression step and a multivariate temporal-regression step. ICs were selected according to the HCP-rsfMRI template (Whitfield-Gabrieli and Nieto-Castanon 2012) and inserted in a group analysis.

DTI preprocessing: includes correction of eddy current-induced distortions with non-linear approximation (Andersson and Sotiropoulos 2016); brain extraction using the BET tool (Smith 2002); image registration of volume B0 with ICBM-DTI-81 atlases (Mori et al. 2008) in two stages, the first with affine image registration of 12 degrees of freedom and second stage of non-linear alignment with spline interpolation.

After the creation of spatial transformations in volume B0, the tensor field was also adjusted to the standard space (MNI-152 brain template with 2 mm spatial resolution). From the tensor maps, the bayesian diffusion parameters offered by the BEDPOSTX (Behrens et al. 2003) were attached to the PROBTRACKX (Behrens et al. 2003, 2007) method to create a set of probabilistic tractography reconstruction models. The brain white matter tracts were represented in the DTI image volume with the following parameters: step size = 0.70, inertia = 0, fractional anisotropy (FA) less than 0.1 (Taoka et al. 2009; Buchanan et al. 2020; Plaisier et al. 2014); projection threshold = 0.55, the minimum angle between consecutive paths greater than 30° and a posteriori probability of at most two sets of fibers per voxel (Behrens et al., 2003). With the reconstruction of the white matter of the entire brain, it is possible to assemble the adjacency matrix from both brain templates, i.e., the ROIs of the functional atlas and the regions defined by the group of deaf individuals using the ICA analysis. The multiple brain templates mask were applied on the FDT tool which assists the ROI-to-ROI connectivity analysis and both the DTI and fMRI data were spatially normalized using an affine transformation to allow the connectivity cross-comparison. The streamline density was considered with the ROI size normalization to avoid ROI size influence in the connectivity measures.

In both functional and structural brain analyses, the level of statistical significance was defined as $p = 0.05$, corrected for multiple comparisons by False Discovery Rate (FDR) method.

Results

Functional connectivity (FC)

We observed differentiation in the FC pattern when comparing the control group with the deaf group, suggesting adaptive flexibility in several aspects of the resting-state networks (**Fig1**). More specifically, when we focus on the DMN nodes, composed by the Posterior Cingulate Cortex (PCC), medial Prefrontal Cortex (mPFC), and right and left lateral parietal regions (rLP and ILP, respectively).

It is worth highlighting that the connections involving the PCC node were the most affected by hearing deprivation. In deaf individuals, the PCC showed higher connectivity with visual and motor networks, evidencing the central role of this cortical region in the interconnection between sign language-related activities. It also showed a lower FC with salience networks, which are associated with focus and attention activity and language networks. The other DMN nodes were also affected due to deafness, however to a minor extent. The right LP node in deaf presented lower FC with salience and dorsal attentional networks when compared to the hearing group, while there was a higher FC with the frontoparietal network. Finally, the mPFC node in deaf showed lower FC with the visual network and higher FC with the frontoparietal network when compared to the hearing group. It was also found prominence of functional connectivity changes in the right hemisphere, mostly in the frontoparietal and temporal (superior and medial) lobes. For more information see Supplementary Material.

We also observed significant changes in DMN topology, with a greater spatial extent in the mPFC node as Loading [MathJax]/jax/output/CommonHTML/jax.js and PCC nodes in the deaf group. **Fig2** shows the difference

in the spatial extent of the regions obtained with the ICA ($p\text{-FDR} < 0.05$). In addition, **Table 1** shows the localization coordinates of the center of mass, the number of voxels, and the percentage of volume change of these regions between groups. Brain regions such as the left occipital pole, right frontal medial gyrus, right putamen, and right paracingulate gyrus showed higher volume in congenital deafness when compared to control. On the contrary, the right lateral posterior occipital cortex, right postcentral gyrus and right insular cortex presented lower volume in congenital deaf when compared to control.

Structural connectivity (SC)

Significant differences were found in the SC analysis between deaf and hearing groups (**Fig3**, **Table 2**). It is possible to notice a tendency towards changes in the posterior portion of the brain, showing preponderant changes in the occipital and parietal lobes. It is also noted that there are several regions of white matter with differences in streamline density involving both classical signal language support regions (e.g., language and visual networks) as well as concentrated networks for focus activity, attention, and cognitive filtering (e.g., dorsal attentional and salience networks). For more information see Supplementary Material

Discussion

The objective of this study was to assess the structural and functional brain organization of deaf individuals at a resting state. The deaf group presented higher FC among salience, dorsal attentional, and frontoparietal networks when compared to the hearing group. Higher FC in regions of these networks, such as right and left supramarginal gyri (SMG; salience nodes), intraparietal sulcus and frontal eye fields (dorsal attentional nodes), and right and left lateral prefrontal cortex (LPFC; frontoparietal nodes), suggests that such self-organized resting-state networks are more strongly connected in the deaf group to supply the hearing deficit.

Previous studies have hypothesized that changes in functional networks are related to hearing adaptation. Wenjing et al (2015) related increased connectivity between the limbic system and regions involved in visual and language processing in deaf prelingual adolescents compared to the deaf postlingual group which revealed that the reorganization of brain functional networks occurred in prelingually deaf adolescents to adapt to deficient auditory input. Higher FC in the right posterior frontal lobe, right precentral gyrus, right supramarginal gyrus, and left posterior cingulate cortex were found in subjects that lost hearing by using ototoxic drugs when compared to a normal hearing group (Zhengliang et al 2015). Menon and Uddin (2010) stated that the salience network has a regulatory function, serving as a filter between environmental stimuli and the decision-making processes involving cognitive control, attention, and emotional responses. The dorsal attentional network plays a central role in activities that require focus and attention (Power et al. 2014) and may be linked to mental processes such as working memory, episodic memory, and mental images (Lückmann et al. 2014). In addition, the frontoparietal

Loading [MathJax]/jax/output/CommonHTML/jax.js g processes, basic attentional activities, and environmental

monitoring (Codina et al. 2011; Lückmann et al. 2014). Higher functional connectivity in such networks in deaf suggests more responsiveness to a visual environmental stimulus due to the lack of hearing, urging more attention, and focus on perceiving, processing, and responding to the visual input.

FC in the visual and sensorimotor networks was also higher in deaf individuals. Several studies have demonstrated the increased recruitment of visual and motor regions due to the use of sign language (Sacks 1990; Bavelier et al. 2001; Penhune et al. 2003; Bavelier and Hirshorn 2010), and the differences in the visual cortex, mainly related to peripheral vision, were present when there is communication among sign language-aware individuals (Neville and Lawson 1987; Hong Lore and Song 1991). Finally, due to the natural adaptation presented for language representation, mainly due to the need for the use of gestural and visual commands, it is expected that global functional modifications about these networks are present, as seen in our findings.

We also evaluated FC changes in the DMN due to its broad representativeness in various cognitive functions, e.g., its role in monitoring the external environment (Shulman et al. 1997; Raichle and Raichle 2001; Raichle et al. 2001), self-judgment, mental simulations, states of meditation, rambling (Buckner and Vincent 2007; Buckner et al. 2008; Andrews-Hanna 2012), recall of the past, and future planning (Andrews-Hanna, 2012). Higher FC of DMN-PCC node with visual and sensorimotor networks in deaf, suggests more intensive use of visuospatial information for environmental monitoring by deaf individuals (Vogt et al. 1992; Raichle and Raichle 2001). In contrast, lower DMN-PCC connectivity with language network (posterior portion of the superior temporal gyrus – pSTG, and inferior frontal gyrus – IFG) may indicate that, for the basal function in the attention of local events, no linguistic interpretation support is required. Regarding the mPFC region, which presents higher FC with the frontoparietal-LPFC, we can infer a highlight on decision-making activities (Botvinick et al. 2004; Bechara and Damasio 2005; Holroyd et al. 2009) and fine controls (Ridderinkhof et al. 2004; Posner et al. 2007). Other authors also state that mPFC may be linked to emotional or motor response events (Euston et al. 2012).

The salience network, which is also formed by the insula, and the right lateral occipital cortex showed lower FC when the deaf individuals were at rest, suggesting that such areas are less recruited in the resting condition since the representation of external movements and actions are unrelated to the meaning of communication. Neuroimaging studies with hearing individuals show that, in addition to having a strong connection with Broca's area, which is the canonical region of speech production, the insula is also highly connected with other speech and language centers (Oh et al. 2014), showing its role of mediating motor aspects of language production, specifically on articulatory control (Nieuwenhuys 2012).

Additionally, our results indicate the great importance of the right hemisphere in FC adaptations to hearing deprivation. It is well-known that the right hemisphere plays a fundamental role in sign language processing regarding fMRI findings (Neville and Lawson 1987). Deaf individuals who have been exposed to sign language since childhood showed broad activation of the right hemisphere, particularly in the

prefrontal cortex, thus corroborating the proposal that cortical activation of this area may be specifically linked to the linguistic use of surrounding space.

Other findings are also related to the SC differentiation driven by hearing deprivation. Regarding the physical organization of the white matter, the difference between deaf and hearing groups is concentrated in the posterior portion of the brain, with the occipital, parietal, and posterior temporal lobes being mostly affected. Hence, it is noticed that the fascicles that support the classical regions of vision and language were also adapted due to hearing deprivation. Regarding the fascicles connected to the regions of the visual cortex, we can highlight the increased SC of the right visual lateral network with the left dorsal attentional network (IPS). Previous studies have shown that deaf individuals present a larger lateral field of view as well as a faster speed in identifying movements that occur in peripheral planes (Hong Lore and Song 1991; Proksch and Bavelier 2002; Bavelier et al. 2006; Codina et al. 2011, 2017). In addition, an increase in fractional anisotropy has been observed in interhemispheric regions of the visual cortex (Kim et al. 2009), also indicating that congenital deaf people have a higher visual reactivity (regarding faster visual detection), which has been associated with changes in the striate cortex (Bottari et al. 2010). From these findings, we can assume that learning and communicating by using sign language since childhood play an essential role in adapting the SC in the visual cortex, thus supporting the individual in the communication process.

Another interesting finding is the lower SC between the right dorsal attentional network (IPS) with the anterior cerebellar network, and the DMN-PCC with the left language network (pSTG node). Previous studies have shown a decrease in fractional anisotropy values specifically in the superior temporal gyrus, Heschl's gyrus, and splenium of the corpus callosum (Emmorey et al. 2003; Li et al. 2012; Miao et al. 2013). Therefore, we can infer that the left pSTG node presents lower SC due to the absence of auditory stimuli throughout life. It is noteworthy, however, that these findings do not indicate a direct relationship with the inactivity of these cortical areas, as it is widely known that the use of sign language recruits the same classical language brain regions. In other words, when the deaf individual is not focused on communicating with peers, stimulation of the auditory cortex is reduced, making the structured network less densely connected in the region of the language network in the long term.

Our study has some limitations, such as small sample size, lack of a group of bilingual individuals (hearing individuals who communicate by both oral and sign languages) for a triple comparison, and no evaluation of axonal volume loss or fiber disruption which was possible with more accurate images (e.g. HARDI acquisition).

In conclusion, even if brain functional and structural changes are present, mainly in DMN, salience, dorsal attentional, and frontoparietal networks, as well as visual and sensorimotor networks, the deaf people brain can adapt in order to remain functionally and structurally capable for the main human tasks, presenting the same potential seen in the hearing individual. Our study clarifies the main differences of the brain functional and structural connectivity in congenitally deaf individuals, which may enlighten a better understanding of the global brain network organization on hearing deprivation.

Declarations

Funding

This study was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

Acknowledgments

The authors would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the financial support on this research.

Declaration of Competing Interest

None.

Data Availability

Data is not available due to patient confidentiality.

Code Availability

The software and routines used in the present study are all available in their respective references.

Authors' Contributions

Dell Ducas, K. and Senra Filho, A. C. S contributed to study conception, image processing, data analysis, manuscript writing, and revision. Silva, P.H.R. contributed to image processing, analysis, manuscript writing, and revision. Secchinato, K.F contributed to figures presentation and manuscript revision. Leoni, R.F. contributed to manuscript writing and revision. Santos, A.C.Silva contributed to study conception, analysis, discussion, and manuscript revision.

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Tables

Table 1: Topological differences presented in the functional connectivity between deaf and hearing individuals, concerning the Harvard-Oxford cortical atlas.

Cortical region	Center of mass (MNI coordinates)	Number of voxels	Volume changes ^a (%)
left Occipital Pole	-16 -84 -04	176	+2
right Lateral Occipital Cortex	+54 -74 +18	92	-3
right Postcentral Gyrus	+48 -24 +66	51	-1
right Frontal Medial Gyrus	+36 +08 +38	41	+1
right Putamen	+16 +14 -08	40	+3
right Paracingulate Gyrus	+12 +40 +34	23	+1
right Insular Cortex	+34 +20 -02	23	-1

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^a Positive values indicate larger regions in deaf individuals.

Table 2: Differences in structural connectivity between deaf and hearing people.

Resting-State Network Pairs	t-values	p-FDR
Visual Medial - Cerebellar Posterior	3.40	0.001
Visual Medial - Visual Occipital	3.90	0.011
DMN PCC - left Dorsal Attentional IPS	4.64	0.016
right Visual Lateral - left Dorsal Attentional IPS	4.00	0.016
left Dorsal Attentional IPS - right Dorsal Attentional IPS	3.67	0.004
right Salience RPFc - left FrontoParietal LPFC	2.74	0.014
right DMN LP - right Salience SMG	-2.95	0.008
left DMN LP - right Language pSTG	-2.93	0.009
right Dorsal Attentional IPS - Cerebellar Anterior	-3.45	0.003
DMN PCC - left Language pSTG	-2.95	0.011
left Language pSTG - Cerebellar Anterior	-3.39	0.004
Visual Medial - left Language pSTG	-3.02	0.000
DMN PCC - Cerebellar Anterior	-3.81	0.013

DMN: default mode network. PCC: posterior cingulate cortex. IPS: intraparietal sulcus. RPFc: rostral prefrontal cortex. LPFC: lateral prefrontal cortex. LP: lateral parietal. pSTG: posterior Superior Temporal Gyrus.

Figures

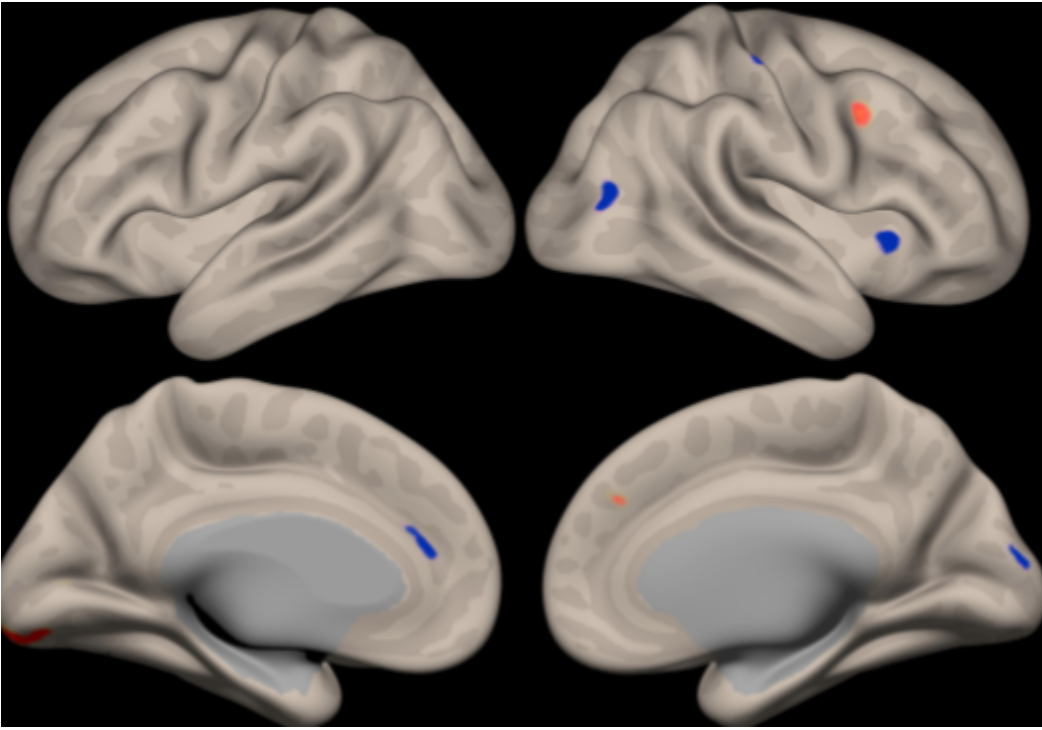


Figure 2

Changes in cortical activation pattern ($p\text{-FDR} < 0.05$) of regions defined by ICA. Orange indicates regions with greater spatial extent in hearing when compared to the deaf group. Blue indicates regions with lower spatial extent in hearing when compared to the deaf group.

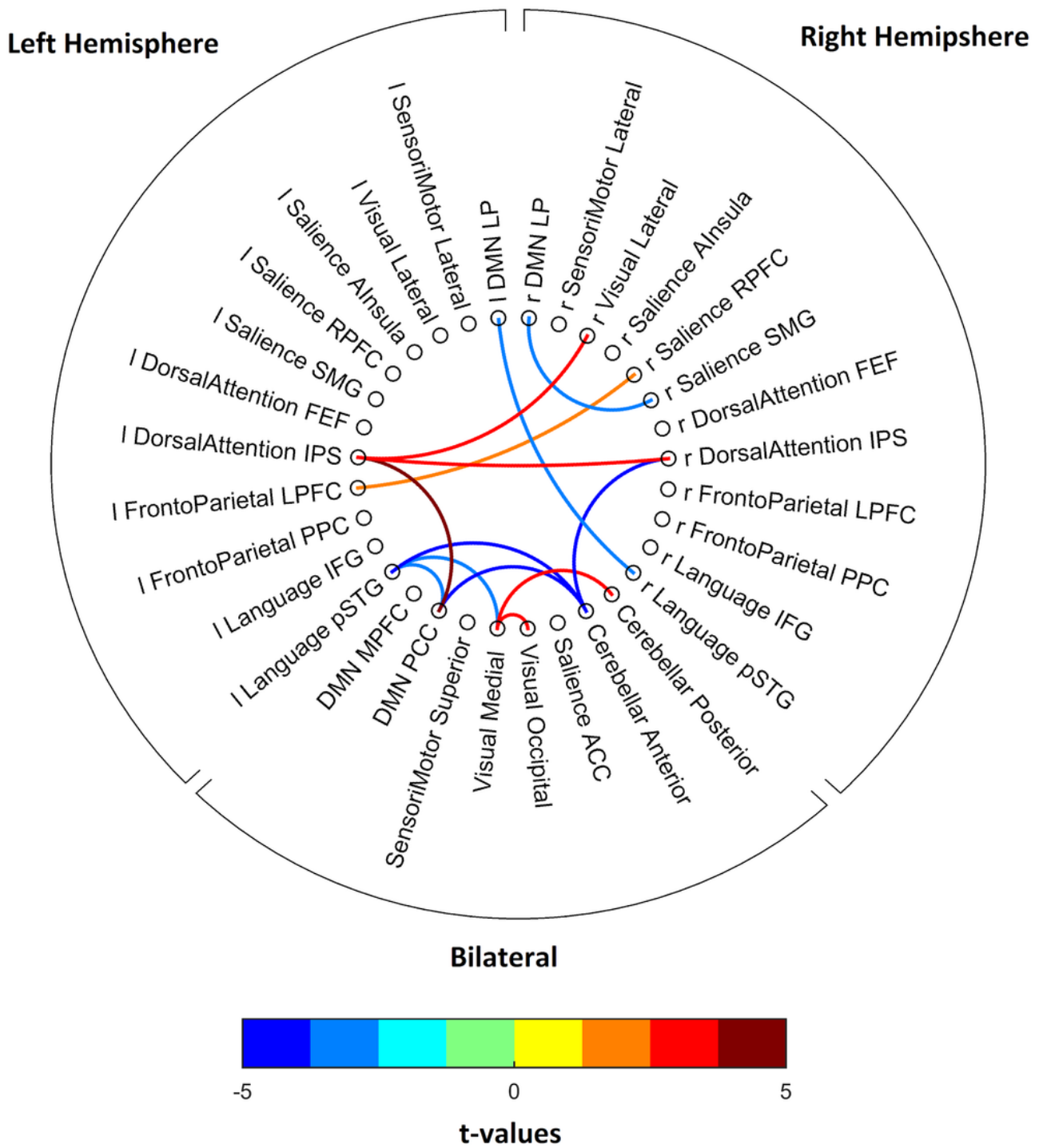


Figure 3

Differences in structural connectivity measured by white matter fiber density between deaf and hearing people (hearing > deaf) ($p\text{-FDR} < 0.05$). Resting-state networks were defined using the Harvard-Oxford atlas. Line colors represent t-values.

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