Functional and structural brain connectivity in congenital deafness

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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 are still an open question. The objective of this study was to investigate the main differences in brain organization manifested in congenitally deaf individuals, concerning the resting-state functional patterns, and white matter structuring. Functional and diffusion 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 among the posterior cingulate cortex node of the default mode network with visual and motor networks, lower functional connectivity 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, 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 demonstrated that the congenital deaf individuals who learned sign language developed significant brain functional and structural reorganization, which provides prominent support for large-scale brain networks associated with attention decision-making, environmental monitoring based on the movement of objects, and on the motor and visual controls.

Keywords Deafness · fMRI · DTI · Brain connectivity · Sign language

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 the 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 region 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 pre-lingual 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 pre-lingual 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 functional and structural connectional reorganization in congenital deaf subjects who learned sign language; 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 pre-lingual deafness (Kim et al. 2014).

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 in networks beyond the auditory cortex, such as the Default Mode Network (DMN), Fronto-Parietal Network (FPN) and Salience Network. Those brain networks are known to be related to cognitive control (Sridharan et al. 2008), and are being suggested as a requirement to a network integration that tries to compensate for the sensorial deficits caused by deafness (Bonna et al. 2020). Hence, it suggests that a change of broader cognitive systems might better reflect the behavioral skills that deaf people develop, rather than function-specific (i.e. language and visuospatial processing). 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 represented by inter-regional network communication could be also affected by hearing deprivation. Therefore, we aimed to assess the main brain adaptations present in congenital deaf individuals who learned sign language regarding their structural axonal organization and functional connectivity in the resting state 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 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 ages ranging from 18 to 45 years old). The data from the control group were 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 image 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 obtained using a 3 T system (Philips Achieva, The Netherlands), adapted with a full-body transmission coil and a dedicated 32-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, 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 min.

**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 remaining DW volumes were registered to the b0 volume. To obtain the probabilistic tractography data, we applied the FSL toolkit, regarding the BEDPOSTX and PROBTRACKX software set, as well described in the official documentation (Behrens et al. 2007). A small adjustment on the default parameters for both software was: (1) BEDPOSTX with projection threshold = 0.55, the minimum angle between consecutive paths greater than 30° and
a posteriori probability of at most two sets of fibres per voxel; (2) PROBTRACKX with 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). Furthermore, with the data collected from the probabilistic tractography, we obtained the structural connectivity adjacency matrix from both brain templates considered using the FDT tool. We used the streamline density as the structural connectivity measure, and it was obtained with the ROI size normalization to avoid ROI size influence in the connectivity measures. Finally, to allow the connectivity cross-comparison, MRI data were spatially normalized using an affine transformation.

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

**Results**

**Functional connectivity (FC)**

We observed differentiation in the FC pattern when comparing the control group with the congenital deaf group, suggesting adaptive flexibility in several aspects of the resting-state networks (Fig. 1; Table 1).

**FC changes involving the Language Network**: Congenital deaf presented higher FC between language network with dorsal attentional and salience networks when compared to controls. More specifically, they had higher FC of the left Language pSTG with the right (p-FDR = 0.035) and left (p-FDR = 0.035) Dorsal Attention IPS and right Salience SMG (p-FDR = 0.035). Congenital deaf also presented higher FC of the left Language IFG with the right Salience SMG (p-FDR = 0.009) and between right Language IFG

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**Fig. 1** Comparison of functional connectivity between the deaf group and the control group. The signal contrast was defined as the control group higher than the deaf group (p-FDR < 0.05). Resting-state networks were defined using the Harvard–Oxford atlas. Line colors represent t-values.
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 changesa (%) |
|-----------------------------------|----------------------------------|------------------|---------------------|
| 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                  |

*Positive values indicate larger regions in deaf individuals.

and left Salience SMG (p-FDR = 0.037) when compared to controls.

**FC changes involving the Visual and Sensorimotor Networks:** Functional changes were found in the higher connectivity of the Superior Sensorimotor Network with the Visual Occipital Network (p-FDR = 0.001), right (p-FDR = 0.019) and left (p-FDR = 0.023) Dorsal Attention FEF Network and DMN mPFC (p-FDR = 0.033) in the congenital deaf when compared to controls. They presented higher FC between the left Lateral SensoriMotor with the right Dorsal Attention FEF Network (p-FDR = 0.031) and the right Lateral Sensorimotor with the left FrontoParietal PPC (p-FDR = 0.048). They also presented higher functional connectivity of the Visual Occipital Network with the right (p-FDR = 0.007) and left (p-FDR = 0.007) Dorsal Attention IPS, right (p-FDR = 0.022) and left (p-FDR = 0.022) Dorsal FEF and DMN ACC (p-FDR = 0.035); and lower FC of the Visual Occipital Network with the right Salience Anterior Insula (p-FDR = 0.022) and right Language IFG (p-FDR = 0.036). Additionally, congenital deaf presented higher functional connectivity of the Visual Medial Network with the right (p-FDR = 0.048) and left (p-FDR = 0.045) FrontoParietal LPFC Network and lower functional connectivity with the DMN mPFC (p-FDR = 0.048) and the right Lateral Sensorimotor Network (p-FDR = 0.048). Congenital deaf presented lower FC between the left Visual Lateral and right Salience SMG (p-FDR = 0.047).

**FC changes involving the DMN:** 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 lLP, respectively), the connections involving the PCC node were the most affected by hearing deprivation. Deaf individuals presented higher connectivity of the DMN PCC with Superior Sensorimotor Network (p-FDR = 0.019), Visual Occipital Network (p-FDR = 0.030) and DMN mPFC (p-FDR = 0.047) and lower connectivity with the right (p-FDR = 0.003) and left (p-FDR = 0.001) Salience SMG, right (p-FDR = 0.016) and left (p-FDR = 0.040) Salience Anterior Insula, right Salience RPFC (p-FDR = 0.016). Salience ACC (p-FDR = 0.017) and both right Language pSTG (p-FDR = 0.018) and IFG (p-FDR = 0.033) Networks. The other DMN nodes were also affected, to a lesser extent, due to deafness. The right LP node in deaf presented lower FC with Salience ACC (p-FDR = 0.019) and right Dorsal Attentional FEF (p-FDR = 0.031) networks when compared to the hearing group, while there was a higher FC with the left FrontoParietal PPC network (p-FDR = 0.032). Finally, the mPFC node in deaf showed higher FC with the right FrontoParietal LPFC Network (p-FDR = 0.001), left FrontoParietal PPC (p-FDR = 0.032), right Salience SMG (p-FDR = 0.047) and lower FC with the Visual Medial Network (p-FDR = 0.048) when compared to the hearing group.

**FC changes involving the Dorsal Attentional Network:** Congenital deaf presented higher FC of the right Dorsal Attention FEF with right (p-FDR = 0.001) and left (p-FDR = 0.001) Dorsal Attentional IPS, right FrontoParietal LPFC (p-FDR = 0.036) when compared to controls. They also presented higher FC of the right Dorsal Attention IPS with the left FrontoParietal PPC (p-FDR = 0.021), right Salience RPFC (p-FDR = 0.021) and right FrontoParietal LPFC (p-FDR = 0.036); higher FC of the left Dorsal Attentional IPS with the right Salience RPFC (p-FDR = 0.0001), right Salience SMG (p-FDR = 0.021), and the right FrontoParietal LPFC (p-FDR = 0.036) when compared to controls.

**FC changes involving the Cerebellar Network:** Congenital deaf presented lower FC of the Posterior Cerebellar with the Salience ACC (p-FDR = 0.041), right Salience RPFG (p-FDR = 0.046) and right (p-FDR = 0.046) and left (p-FDR = 0.046) Salience SMG.

**Additional FC changes involving the FrontoParietal Network:** in addition to the described changes involving FrontoParietal Network with the other networks, congenital deaf presented higher intra-network connectivity between bilateral FrontoParietal LPFC (p-FDR = 0.036).

**Additional FC changes involving the Salience Network:** in addition to the described changes involving Salience Network with the other networks, congenital deaf presented higher intra-network connectivity between bilateral Salience RPFC and left Salience SMG (p-FDR = 0.019).

We also observed significant changes in DMN topology, with the greater spatial extent in the mPFC node as well as lower spatial extent in bilateral LP and PCC nodes in the deaf group. Figure 2 shows the difference in the spatial extent of the regions obtained with the ICA (p-FDR < 0.05). In addition, Table 2 shows the coordinates of the center
of mass, number of voxels, and the percentage of volume change of these regions between groups. Regions, such as the left occipital pole, right frontal medial gyrus, right putamen, and right paracingulate gyrus, showed higher volume in congenital deaf when compared to control. Right lateral posterior occipital cortex, right postcentral gyrus, and right insular cortex presented lower volume in congenital deaf when compared to control.

**Structural connectivity**

Significant differences in white matter tracts were found between deaf and hearing groups (Fig. 3; Table 2).

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**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
Discussion

The objective of this study was to assess the structural and functional brain organization of congenitally 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 pre-lingual adolescents compared to the deaf post-lingual group which revealed that the reorganization of brain functional networks occurred in pre-lingually 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 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 network has been related to decision-making 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 high-light 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 representations 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 interhemi-spheric 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 communicate 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 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.

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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.

Compliance with ethical standards

Conflict of interest  The authors declare that they have no conflicts of interest.

References

Andersson JLR, Sotiropoulos SN (2016) An integrated approach to correction for off-resonance effects and subject movement in diffusion MR imaging. Neuroimage. https://doi.org/10.1016/j.neuroimage.2015.10.019

Andrews-Hanna JR (2012) The brain’s default network and its adaptive role in internal mentation. Neuroscientist 18(3):251–270

Assemblal HE, Tschumperle D, Brun L, Siddiqi K (2011) Recent advances in diffusion MRI modeling: angular and radial reconstruction. Med. Image Anal 15(4):369–396

Bavelier D, Hirshorn EA (2010) I see where you’re hearing: How cross-modal plasticity may exploit homologous brain structures. Nat Neurosci 13(11):1309–1311

Bavelier D, Brozinsky C, Tomann A et al (2001) Impact of early deafness and early exposure to sign language on the cerebral organization for motion perception. J Neurosci. https://doi.org/10.1523/jneurosci.21-22-08931.2001

Bavelier D, Dye MWG, Hauser PC (2006) Do deaf individuals see better? Trends Cogn Sci 10(11):512–518

Bechara A, Damasio AR (2005) The somatic marker hypothesis: a neural theory of economic decision. Games Econ Behav. https://doi.org/10.1016/j.geb.2004.06.010

Behrens TEJ, Woolrich MW, Jenkinson M et al (2003) Characterization and propagation of uncertainty in diffusion-weighted MR imaging. Magn Reson Med. https://doi.org/10.1002/mrm.10609

Behrens TEJ, Berg HJ, Jbabdi S et al (2007) Probabilistic diffusion tractography with multiple fibre orientations: what can we gain? Neuroimage. https://doi.org/10.1016/j.neuroimage.2006.09.018

Bonna K, Fink C, Zimmermann M et al (2020) Early deafness leads to re-shaping of functional connectivity beyond the auditory cortex. Brain Imaging Behav. https://doi.org/10.1007/s11682-020-00346-y

Bottari D, Nava E, Ley P, Pavan F (2010) Enhanced reactivity to visual stimuli in deaf individuals. Restor Neurol Neurosci. https://doi.org/10.3233/RNN-2010-0502

Botvinick MM, Cohen JD, Carter CS (2004) Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn Sci 8(12):539–546

Buchanan CR, Bastin ME, Ritchie SJ, Liewald DC, Madole JW, Tucker-Drob EM, Deary IJ, Cox SR (2020) The effect of network thresholding and weighting on structural brain networks in the UK Biobank. Neuroimage. https://doi.org/10.1016/j.neuroimage.2019.116443

Buckner RL, Vincent JL (2007) Unrest at rest: default activity and spontaneous network correlations. Neuroimage 37(4):1091–1096

Buckner RL, Andrews-Hanna JR, Schacter DL (2008) The brain’s default network: anatomy, function, and relevance to disease. Ann NY Acad Sci. https://doi.org/10.1196/annals.1440.011

Codina C, Buckley D, Port M, Pascalis O (2011) Deaf and hearing children: a comparison of peripheral vision development. Dev Sci. https://doi.org/10.1111/j.1467-7687.2010.01017.x

Codina CJ, Pascalis OL, Baseler HA et al (2017) Peripheral visual reaction time is faster in deaf adults and British Sign Language interpreters than in hearing adults. Front Psychol. https://doi.org/10.3389/fpsyg.2017.00050

Collins DL, Neelin P, Peters TM, Evans AC (1994) Automatic 3d intersubject registration of mr volumetric data in standardized talairach space. J Comput Assist Tomogr. https://doi.org/10.1097/00004728-199403000-00005

Corina DP, San Jose Robertson L, Guillemin A et al (2003) Language lateralization in a bimanual language. J Cogn Neurosci. https://doi.org/10.1162/089892903762523979

de Sobreira ACO, Capo BM, Dos Santos TS, Gil D (2015) Desenvolvimento de fala e linguagem na deficiência auditiva: relato de dois casos. Rev CEFAC 17:308–317

Dobie R, Van Hemel S (2005) Hearing loss: determining eligibility for social security benefits. National Academies Press, USA

Emmorey K, Allen JS, Bruss J et al (2003) A morphometric analysis of auditory brain regions in congenitally deaf adults. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.1730169100

Euston DR, Gruber AJ, McNaughton BL (2012) The role of medial prefrontal cortex in memory and decision making. Neuron 76(6):1057–1070

Friston KJ, Holmes AP, Worsley KJ et al (1994) Statistical parametric maps in functional imaging: A general linear approach. Hum Brain Mapp. https://doi.org/10.1002/hbm.460020402
Gazzaniga MS (2000) The new cognitive neuroscience
Holroyd CB, Krigolson OE, Baker R et al (2009) When is an error not a prediction error? An electrophysiological investigation. Cogn Affect Behav Neurosci. https://doi.org/10.3758/CABN.9.1.59
Hong Lore W, Song S (1991) Central and peripheral visual processing in hearing and nonhearing individuals. Bull Psychon Soc. https://doi.org/10.3758/BF0333966
IBGE (2002) Censo Demográfico 2000. Universo
Jenkinson M, Beckmann CF, Behrens TEJ et al (2012) Fsl. Neuroimage 62:782–790. https://doi.org/10.1016/j.neuroimage.2011.09.015
Kim DJ, Park SY, Kim J et al (2009) Alterations of white matter diffusion anisotropy in early deafness. NeuroReport. https://doi.org/10.1097/WNR.0b013e3282d0eed
Kim E, Kang H, Lee H, Lee H-J, Suh M-W, Song J-J, Oh S-H, Lee DS (2014) Morphological brain network assessed using graph theory and network filtration in deaf adults. Hear Res. https://doi.org/10.1016/j.heares.2014.06.007
Li Y, Ding G, Booth JR et al (2012) Sensitive period for white-matter connectivity of superior temporal cortex in deaf people. Hum Brain Mapp. https://doi.org/10.1002/hbm.21215
Lückmann HC, Jacobs HIL, Sack AT (2014) The cross-functional role of the insular cortex. a review. Prog Brain Res
Neville HJ, Lawson D (1987) Attention to central and peripheral visual processing in deaf and hard-of-hearing children: a comparison of sensory and nonsensory tasks. J Cogn Neurosci. https://doi.org/10.2307/2073251
Neville H, Bavelier D (2002) Human brain plasticity: evidence from sensory deprivation and altered language experience. Prog Brain Res 138:177–188
Neville HJ, Bavelier D (2002) Human brain plasticity: evidence from sensory deprivation and altered language experience. Prog Brain Res
Nicoletti S, Gasperini S, Iedema P et al (2000) Speech perception in deaf children: a PET study. J Cogn Neurosci 12:283–292
Petito LA (1994) Are signed languages “real” languages? Evidence from American sign language and langue des signes Quebequoise. Signpost 7(3):1
Petito LA, Zatorre RJ, Gauna K et al (2000) Speech–like cerebral activity in profoundly deaf people processing signed languages: Implications for the neural basis of human language. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.97.25.13961
Pieper S, Lorenzens B, Schroeder W, Kikinis R (2006) The NA-MIC Kit: IKT, VTK, pipelines, grids and 3D slicer as an open platform for the medical image computing community. In: 2006 3rd IEEE international symposium on biomedical imaging: from nano to macro—proceedings
Plaisier A, Pieterman K, Lequin MH, Govaert P, Heemskerk AM, Reiss IKM, Krestin GP, Leemans A, Dudink J (2014) Choice of diffusion tensor estimation approach affects fiber tractography of the fornix in preterm brain. Am J Neuroradiol 35:1219–1225. https://doi.org/10.3174/ajnr.A3830
Posner MI, Rothbart MK, Sheese BE, Tang Y (2007) The anterior cingulate gyrus and the mechanism of self-regulation. Cogn Affect Behav Neurosci 7(4):391–395
Power JD, Schlaggar BL, Petersen SE (2014) Studying brain organization via spontaneous fMRI signal. Neuro 84(4):681–696
Proksch J, Bavelier D (2002) Changes in the spatial distribution of visual attention after early deafness. J Cogn Neurosci. https://doi.org/10.1162/08989290260138591
Raiche ME, Raiche ME (2001) Searching for a baseline: functional imaging and the resting human brain. Nat Rev Neurosci. https://doi.org/10.1038/35094500
Raiche ME, MacLeod AM, Snyder AZ et al (2001) A default mode of brain function. Proc Natl Acad Sci USA 98:676–682. https://doi.org/10.1073/pnas.98.2.676
Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S (2004) The role of the medial frontal cortex in cognitive control. Science 306(5695):443–447
Rondinoni C, Amrao Junior E, Cendes F, Santos AC, Salomão CEG (2013) Effect of scanner acoustic background noise on strict resting-state fMRI. Braz J Med Biol Res 46:359–367. https://doi.org/10.1590/1414-431X20123799
Sacks O (1990) Seeing voices: a journey into the world of the deaf. Contemp Sociol. https://doi.org/10.2307/2073251
Schick B, Marschark M, Spencer PE (2010) Advances in the sign-language development of deaf children. Oxford University Press, Oxford
Shulman GL, Fiez JA, Corbetta M et al (1997) Common blood flow and network filtration in deaf adults. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.94.21.11574
Smith SM (2002) Fast robust automated brain extraction. Hum Brain Mapp. https://doi.org/10.1002/hbm.21032
Shulman GL, Fiez JA, Corbetta M et al (1997) Common blood flow and network filtration in deaf adults. Proc Natl Acad Sci USA. https://doi.org/10.1073/pnas.94.21.11574
Sridharan D, Levitin DJ, Menon V (2008) A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. Proc Natl Acad Sci USA 105:12569–12574. https://doi.org/10.1073/pnas.080005105
Taoka T, Morikawa M, Akashi T, Miyasaka T, Nakagawa H, Ikuchi K, Kishimoto T, Chikikawa K (2009) Fractional anisotropy-threshold dependence in tract-based diffusion tensor analysis: evaluation of the uncinate fasciculus in Alzheimer disease. Am J Neuroradiol 30:1700–1703. https://doi.org/10.3174/ajnr.A1698
Vogt BA, Finch DM, Olson CR (1992) Functional heterogeneity in cingulate cortex: The anterior executive and posterior evaluative regions. Cereb Cortex. https://doi.org/10.1093/cercor/2.6.435-a

Wenjing L, Jianhong L, Jieqiong W, Zhou P, Zhenchang W, Junfang X, Huiguang H (2015) Functional reorganizations of brain network in prelingually deaf adolescents. Neural Plast. https://doi.org/10.1155/2016/9849087

Whitfield-Gabrieli S, Nieto-Castanon A (2012) Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. Brain Connect 2:125–141. https://doi.org/10.1089/brain.2012.0073

Wolak T, Cieśla K, Pluta A, Włodarczyk E, Biswal B, Skarżyński H (2019) Altered functional connectivity in patients with sloping sensorineural hearing loss. Front Hum Neurosci 13:284. https://doi.org/10.3389/fnhum.2019.00284

World Health Organization N (2008) The Global Burden of Disease: 2004 update

Zhengliang L, Qingfeng Z, Zuojun G, Zhenhu S, Lixin W, Wang Y (2015) Study of functional connectivity in patients with sensorineural hearing loss by using resting-state fMRI. Int J Clin Exper Med 8:569–578

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