Resting-state functional connectivity in deaf and hearing individuals and its link to executive processing

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ABSTRACT

Sensory experience shapes brain structure and function, and it is likely to influence the organisation of functional networks of the brain, including those involved in cognitive processing. Here we investigated the influence of early deafness on the organisation of resting-state networks of the brain and its relation to executive processing. We compared resting-state connectivity between deaf and hearing individuals across 18 functional networks and 400 ROIs. Our results showed significant group differences in connectivity between seeds of the auditory network and most large-scale networks of the brain, in particular the somatomotor and salience/ventral attention networks. When we investigated group differences in resting-state fMRI and their link to behavioural performance in executive function tasks (working memory, inhibition and switching), differences between groups were found in the connectivity of association networks of the brain, such as the salience/ventral attention and default-mode networks. These findings indicate that sensory experience influences not only the organisation of sensory networks, but that it also has a measurable impact on the organisation of association networks supporting cognitive processing. Overall, our findings suggest that different developmental pathways and functional organisation can support executive processing in the adult brain.

1. Introduction

The capacity of the brain for functional and structural reorganisation is known as neural plasticity. Human congenital deafness results in distinct anatomical and functional changes in the brain (Cardin et al., 2020; Simon et al., 2020), and it can provide unique insights into our understanding of brain function and plasticity. Research on deafness and crossmodal plasticity, the adaptive reorganisation of neurons to respond to different sensory inputs (Frasnelli et al., 2011), often focuses on the impact of deafness on sensory processing. However, studying congenital deafness can also help to explain how different sensory developmental experiences impact the organisation of cognitive networks in the brain. In this study, our aim is to investigate the organisation of brain networks

during rest in deaf and hearing individuals, and how this is linked to behavioural performance in executive function tasks.

One approach to studying brain networks is to measure their organisation and functional connectivity using resting-state fMRI. Functional connectivity during resting-state fMRI exploits the temporal dependency of the activity of segregated anatomical regions during rest, when the low-frequency fluctuations of spontaneous activity among functionally related areas are highly correlated (Biswal et al., 1997). The advantage of this technique is that it allows the characterisation of all the components of a functional network, and not only of those which are recruited by specific tasks. As such, resting-state functional connectivity has been used successfully in the characterisation of functional association networks involved in executive functions and cognitive control.

For example, a network of frontal and parietal regions, known as control, central-executive or fronto-parietal network, is usually activated during the performance of cognitively demanding tasks (Cohen and D'Esposito, 2016; Niendam et al., 2012). Activity between the nodes of such networks is also highly correlated during resting-state fMRI (Vincent et al., 2008). Furthermore, performance in executive functions (EF) tasks (outside the MRI scanner) correlates with the level of connectivity between the nodes of the control network during rest (Reineberg et al., 2015; Seeley et al., 2007). Similar links between connectivity at rest and performance in executive function tasks have also been found between other networks of the brain. The salience network is involved in detecting relevant environmental information (Uddin, 2015), and the degree of uncoupling at rest between this network and the default mode network (DMN) is also predictive of performance in executive function tasks in neurotypical individuals and in patients with Parkinson's disease (Putcha et al., 2016).

Understanding how the connectivity of these functional networks is linked to executive performance in deaf individuals can further our knowledge of how sensory experience modulates brain organisation and function. Animal studies suggest that congenital deafness results in significant changes in functional connectivity between auditory areas after induced stimulation (Kral et al., 2017; Yusuf et al., 2020). However, in humans, the intrinsic (within-network) connectivity of the auditory network at rest, measured with resting-state fMRI, seems to be largely preserved in deaf individuals (Striem-Amit et al., 2016). When differences in intrinsic connectivity have been found, they have likely been due to different language experience rather than different sensory experience (Li et al., 2013). In contrast, several studies of resting-state fMRI in deaf and hearing individuals have found differences in connectivity between the auditory cortex and other cortical regions, suggesting that sensory experience shapes the functional interaction of this region with other brain networks (Andin and Holmer, 2022; Bonna et al., 2021; Cardin et al., 2018; Dell Ducas et al., 2021; Ding et al., 2016; Kumar et al., 2021). These findings include differences between deaf and hearing individuals in resting-state connectivity between auditory and fronto-parietal regions involved in higher-order cognition and executive processing, supporting claims that sensory experience shapes cognitive processing in the brain (Andin and Holmer, 2022; Cardin et al., 2018; Ding et al., 2016). Enhanced functional connectivity during rest in deaf individuals has been found between the superior temporal gyrus (STG) and components of the salience network, such as the bilateral anterior insula and the dorsal anterior cingulate cortex (Ding et al., 2016). Furthermore, the functional connectivity of the STG predicted performance in a WM task (Ding et al., 2016). Increased resting-state connectivity has also been found between left superior temporal cortex (STC) and fronto-parietal regions such as the pre-supplementary motor area (pre-SMA) and the dorsolateral prefrontal cortex (DLPFC). In fact, Andin and Holmer (2022) found that most differences in network connectivity between deaf and hearing individuals were localised to middle and superior temporal areas. These results, together with evidence showing that auditory areas are recruited during some visual executive function tasks in deaf individuals (Cardin et al., 2018; Ding et al., 2015; Manini et al., 2022), suggest a role for auditory areas in specific subcomponents of executive processing as a consequence of deafness (Manini et al., 2022).

Differences in functional connectivity between deaf and hearing individuals are not restricted to auditory sensory regions, but have also been found between other networks of the brain. Bonna et al. (2021) found differences between deaf and hearing individuals in connectivity between control, DMN, visual, subcortical, memory, salience, ventral attention and somatomotor networks. Kumar et al. (2021) reported increased connectivity between the salience network and left auditory regions in deaf individuals, but also differences that extended beyond the auditory cortex, including increased connectivity between the salience network and the bilateral anterior insula, between the DMN and the left middle cingulate cortex, and between the somatomotor network

and the left cerebellum. In deaf adolescents, Li et al. (2015) observed increased connectivity between the right superior parietal cortex and the right insula, and between the left middle temporal gyrus and the right posterior cingulate gyrus. They also found reduced connectivity between the right superior parietal cortex and the left middle orbito-frontal cortex, and between the right postcentral gyrus and the *pars opercularis* of the left inferior frontal gyrus.

Overall, findings from task- and resting-state fMRI studies comparing deaf and hearing individuals show: 1) evidence of cognitive processing in auditory areas in deaf individuals; and 2) a change in the organisation and functional connectivity of association networks. These findings suggest that developmental auditory sensory experience could impact the organisation of cognitive processing in the brain. Here we studied the effect of sensory experience on brain organisation in deaf and hearing individuals, focusing on how differences in resting-state functional connectivity are linked to performance in executive function tasks. It has been shown that, in deaf individuals, auditory regions can be recruited for some higher-order cognitive tasks (Buchsbaum et al., 2005; Cardin et al., 2018; Ding et al., 2015; Manini et al., 2022). Here we are interested in understanding whether network states are also reorganised by sensory experience, being reflected in the connectivity between auditory areas and association networks. To study this, we measured resting state connectivity in deaf and hearing individuals, and performance in three standardised executive function tasks: visual working memory, inhibition and switching. We predict that, in hearing and deaf individuals, performance in EF tasks will be correlated with the strength of connectivity of association networks. We hypothesise that in addition to this, deaf individuals will also show a link between performance in the EF tasks and connectivity between components of the auditory and association networks, such as the control and salience networks. These networks have been found to be functionally connected to auditory areas in resting state studies in deaf individuals (Andin and Holmer, 2022; Cardin et al., 2018; Ding et al., 2016). A correlation between connectivity strength and performance across all tasks would suggest an involvement in cognitive control of auditory regions in deaf individuals. In addition, switching tasks have pointed towards a role of the salience networks in shifting between states (Menon and Uddin, 2010; Sridharan et al., 2008). We have previously found increased activation of auditory regions during switching, suggesting that this could be a potential role of the reorganised superior temporal cortex of deaf individuals (Manini et al., 2022). A correlation between performance in the switching task and connectivity between auditory and salience networks would support this hypothesis.

2. Methodology

2.1. Participants

Data were acquired from 19 severely or profoundly deaf individuals and 19 hearing individuals, who were scanned at the Moscow Research Centre of Neurology. Deaf and hearing participants were recruited through the Galina Zaitseva Centre for Deaf Studies and Sign Language. Deaf participants were congenitally deaf or had become deaf in infancy (Table 1). They were all proficient signers of Russian Sign Language (RSL). Hearing participants were native speakers of Russian, and fully qualified RSL interpreters or advanced students of RSL at the Galina Zaitseva Centre for Deaf Studies and Sign Language. These two groups were chosen as members of both were bilingual in a signed and spoken language.

All participants were right-handed (self-reported) and had full or corrected vision.

Data from four participants were excluded from the analysis for the following reasons: a) excessive motion during scanning (i. e. change in motion parameters was more than 1 mm in >20% of the scans): 2 deaf participants; b) data corruption during scanning: 1 hearing participant; c) potential delay in first language acquisition: 1 deaf participant. Thus,

Table 1
Language background of deaf participants.

Onset of deafness	Cause of deafness	Level of RSL (1–7)	Age of RSL acquisition	Preferred language	Hearing status		Form of communication	
					1ary carer	2ary carer	1ary carer	2ary carer
from birth	hereditary	7	from birth	RSL	deaf	deaf	RSL, SSR, fingerspelling	RSL
from birth	hereditary	7	from birth	RSL	deaf	deaf	RSL	RSL
from birth	hereditary	7	12–14years	RSL, OR	hearing	deaf	OR	SSR
from birth	hereditary	7	from birth	RSL	deaf	deaf	RSL	RSL
from birth	hereditary	7	from birth	RSL	deaf	HoH	RSL	OR; SSR
from birth	hereditary	7	from birth	RSL	HoH	deaf	RSL, SSR, fingerspelling WR	RSL
from birth	hereditary	6	before 3	RSL	deaf	deaf	RSL	RSL
from birth	hereditary	7	before 3	RSL	deaf	deaf	RSL	RSL
from birth	hereditary	7	from birth	RSL	deaf	deaf	RSL, SSR, fingerspelling	RSL, SSR, fingerspelling
from birth	hereditary	7	from birth	SSR	deaf	deaf	SSR	SSR
before 3	antibiotics	7	from birth	RSL	HoH	deaf	RSL, SSR	RSL
before 3	antibiotics	6	3–5years	OR	hearing	hearing	fingerspelling, OR	fingerspelling, OR
before 3	antibiotics	6	3–5years	RSL	hearing	hearing	OR	OR
before 3	antibiotics	5	before 3	SSR	deaf	deaf	SSR	RSL
before 3	antibiotics	7	from birth	RSL, OR	HoH	HoH	RSL	RSL
3–5years	unknown	7	3–5years	RSL	deaf	deaf	RSL, SSR, fingerspelling	RSL, SSR, fingerspelling

Level of RSL is self-reported. RSL: Russian Sign Language; OR: Oral Russian; SSR: sign-supported Russian; WR: written Russian; HoH: hard-of-hearing.

the following participants were included in the analysis: 1) 16 deaf participants (8 female, 8 male; age = 33.37 +- 7.98 SD years, range 19–52 years old) and 2) 18 hearing participants (12 female, 6 male; age = 32 +- 11.05 years; range 19–54 years old). One hearing participant did not complete the behavioural session of the experiment; their data are included in the group comparison that does not include covariates (see below). Two additional participants in the hearing group did not complete the visuospatial working memory task.

All procedures followed the principles of the Declaration of Helsinki. Ethics approval was obtained from the Ethics Committee of the Research Centre of Neurology and from the Rector of the Moscow State Linguistics University. Information about the project and scanning procedures was provided in written Russian and in RSL. Written consent was obtained from all participants before taking part in the project.

2.1.1. MRI data acquisition

MRI data was acquired with a 3 T Magnetom Verio Siemens MRI scanner. Resting state functional imaging data were acquired using a gradient-echo EPI sequence (36 slices, TR = 2400ms, TE = 30ms, FoV = 192, slice thickness = 3 mm, distance factor = 25%) giving a notional resolution of 3 x 3 × 3.75 mm. Each scan lasted 7 min 42 s (190 vol). During this scan, participants were instructed to lie quietly with their eyes open, let their mind wander and not fall asleep. A high-resolution structural scan was also acquired using magnetization-prepared rapid acquisition with gradient echo (MPRAGE, TR = 2300ms, TE = 2.987ms, 1 x 1 × 1 mm resolution, 160 slices).

2.1.2. Resting state connectivity analysis

Seed-to-seed resting-state functional connectivity analysis was carried out in the CONN toolbox implemented in MATLAB (Whitfield-Gabrieli and Nieto-Castanon, 2012). The images were preprocessed using CONN's standard pipeline. The signal fluctuations over time in the resting-state scans were averaged over all the voxels in each ROI and extracted for subsequent correlation analyses. Movement parameters were derived from the realignment of the images and included in the model as regressors of no interest. In addition, the Artifact Detection Tools (ART) toolbox (www.nitrc.org/projects/artifact_detect) was used to assess additional motion and noise artefacts in the data, which were added into subsequent analyses as additional regressors to correct for motion artefacts (CompCor method) (Behzadi et al., 2007; Chai et al., 2012). Lastly, a band-pass filter of 0.008–0.09 Hz was applied to discard cardiovascular and respiratory noise (Chai et al., 2012). The averaged

signal from each ROI (seed) was then correlated with the signal of every other ROI (target), and normalised using Fisher's r-to-z transforms.

Correlation coefficients from each participant were entered into a 2nd-level model with group (deaf, hearing) as a between-subject factor. Results from the performance in the executive function behavioural tasks (see below) were included as covariates in a separate 2nd-level model. All statistical tests were corrected for multiple comparisons by using seed-level FDR-corrected $p < .05$ p-value using Benjamini and Hochberg's algorithm (Benjamini and Hochber, 1995), as implemented in the CONN toolbox.

ROIs consisted of 400 brain parcellations grouped into 17 functional networks (Schaefer et al., 2018). These parcellations were obtained from resting state data from 1489 participants, validated across several resting state and task fMRI protocols, and are publicly available on GitHub (https://github.com/ThomasYeoLab/CBIG/tree/master/stable _projects/brain_parcellation/Schaefer2018_LocalGlobal). Images of the parcellations and network classification overlaid on inflated brains can be found in the Schaefer et al. (2018) paper and here: (https://github. com/ThomasYeoLab/CBIG/blob/master/stable_projects/brain_pa rcellation/Schaefer2018_LocalGlobal/readme_figures/Schaefer2 018_400parcel_parcellation_match_Yeo_17_network_fslr32k.png). The original grouping of Schaefer et al. (2018) does not include a language network, and contains some auditory areas grouped in a temporo/parietal network, with other auditory areas grouped with somatosensory and motor regions in the somatomotor B network. Isolating the connectivity of the auditory and language networks was important for the aims of our study, and to identify any potential effects of a different language experience between groups in our results. In their everyday life, deaf participants in this study mainly use visual strategies for language, such as sign language or lipreading, while hearing participants will use a combination of auditory and visual strategies. To define these networks, we grouped all auditory areas of the temporoparietal and somatomotor B network into a single auditory network. In addition, we identified language regions using Neurosynth's meta-analysis maps for the terms 'language' and 'linguistic' (https://neurosynth.org). ROIs with coordinates falling within regions identified in the meta-analysis were classified into a language network (Table 2). ROIs with coordinates matching those of Tomasi and Volkow (2012)'s definition of Wernicke's area were also classified as part of the language network. In total, our analysis contained 18 functional networks: auditory, language, visual central, visual periphery, somatomotor A and B, dorsal attention A and B, salience/ventral attention A and B, limbic A and B, control A, B and C,

Table 2
Reassignment of ROIs into the auditory and language networks.

Network	Original network assignment and name	Hemisphere	Centroid MNI coordinates
Auditory	TempPar_1	Left	[-52 6–12]
Auditory	TempPar_2	Left	[-60 -12 -2]
Auditory	TempPar_3	Left	[-62 -32 6]
Auditory	TempPar_4	Left	[-52 -44 4]
Auditory	TempPar_5	Left	[-58 -54 10]
Auditory	TempPar_6	Left	[-58 -48 16]
Auditory	SomMotB_Aud_1	Left	[-50 -10 0]
Auditory	SomMotB_Aud_2	Left	[-56 -22 8]
Auditory	SomMotB_Aud_3	Left	[-58 -36 16]
Auditory	SomMotB_Aud_4	Left	[-40 -36 14]
Auditory	TempPar_1	Right	[48 16–20]
Auditory	TempPar_2	Right	[54–4 -20]
Auditory	TempPar_3	Right	[48–20 -8]
Auditory	TempPar_4	Right	[62–18 0]
Auditory	TempPar_5	Right	[50–34 2]
Auditory	TempPar_6	Right	[60–46 6]
Auditory	TempPar_7	Right	[52–40 12]
Auditory	TempPar_8	Right	[64–34 10]
Auditory	TempPar_9	Right	[54–46 20]
Auditory	TempPar_10	Right	[62–40 22]
Auditory	SomMotB_Aud_1	Right	[52 4–6]
Auditory	SomMotB_Aud_2	Right	[54–4 6]
Auditory	SomMotB_Aud_3	Right	[60–24 10]
Language	SalVentAttnA_ParOper_2	Left	[-58 -44 28]
Language	SalVentAttnA_FrOper_2	Left	[-52 8 14]
Language	ContA_PFClv_1	Left	[-48 36 10]
Language	ContA_PFCl_1	Left	[-50 6 26]
Language	ContA_PFCl_2	Left	[-44 20 26]
Language	DefaultB_Temp_4	Left	[-56 -8 -14]
Language	DefaultB_Temp_5	Left	[-60 -34 -4]
Language	DefaultB_Temp_6	Left	[-52 -22 -6]
Language	DefaultB_PFCv_3	Left	[-46 32–10]
Language	DefaultB_PFCv_4	Left	[-48 28 0]
Language	DefaultB_PFCv_5	Left	[-54 20 12]
Language	DefaultB_IPL_2	Left	[-42 -72 44]

and default mode (DMN) A, B and C. Throughout this paper, networks that are anatomically and functionally distinct from motor, sensory or language networks are referred to jointly as association networks (Yeo et al., 2011). These include dorsal attention A and B, salience/ventral attention A and B, limbic A and B, control A, B and C, and default mode (DMN) A, B and C.

2.1.3. Behavioural tasks

Visuospatial Working Memory: To measure visuo-spatial working memory we used a computerized version of the Corsi Block-Tapping Task Corsi (1972); (Kessels et al., 2000), as implemented in the Psychology Experiment Building Languages (PEBL) software (Mueller and Piper, 2014). During the test, participants watched a sequence of squares lighting up in different positions on the screen. Participants were asked to reproduce the order in which the blocks lit up by clicking on the blocks with a computer mouse. For each participant, a Corsi block span score was calculated as the longest sequence that was recalled correctly.

Inhibition: We used a computerized version of the classic Simon Task (Lu and Proctor, 1995), as implemented in PEBL (Mueller and Piper, 2014). During this task, participants responded to a coloured circle appearing either on the left side of the screen, the right side of the screen or in the neutral zone in the middle of the computer screen. The colour of the circles was the relevant aspect of the stimuli, whereas their position was irrelevant for the task. The participant had to respond to red circles with their left hand and to blue circles with their right hand. Participants were instructed to ignore the location of the circles and focus only on their colour.

In the congruent condition, the button press response was spatially congruent with the location of the stimuli (e.g. a right hand response for a stimulus appearing on the right side of the screen). In the incongruent condition, the correct answer was in the opposite location with respect

to the stimulus (e.g. a left hand response for a stimulus appearing on the right side of the screen). An inhibition effect is calculated by subtracting the time in the congruent condition from that in the incongruent condition (inhibition effect = RT incongruent – RT congruent).

Switching: We used the Colour Trail Test (CTT; (D'Elia et al., 1996), a language-free version of the previously developed Trail Making Test (TMT). The CTT was used because it was developed to be free from any language influence and cultural factors; this is important in testing executive functions in deaf people (Atkinson et al., 2015). The test was administered on paper, and consists of numbered circles with pink or yellow backgrounds. The test has two parts: A and B. During part A, the participant is instructed to connect circles numbered 1–25 in sequence as quickly as possible without making a mistake. In part B, participants have to draw a line between the circles numbered 1–25 but alternating between pink and yellow circles: the line should go from the pink 1 to the yellow 2, to pink 3, etc. The interference index was calculated as the time difference in completing part B minus the time taken to complete part A (TB - TA). This difference minimises the contribution of visuospatial and working memory demands in the TA and TB components, and represents a good index of task switching and executive control (Sánchez-Cubillo et al., 2009).
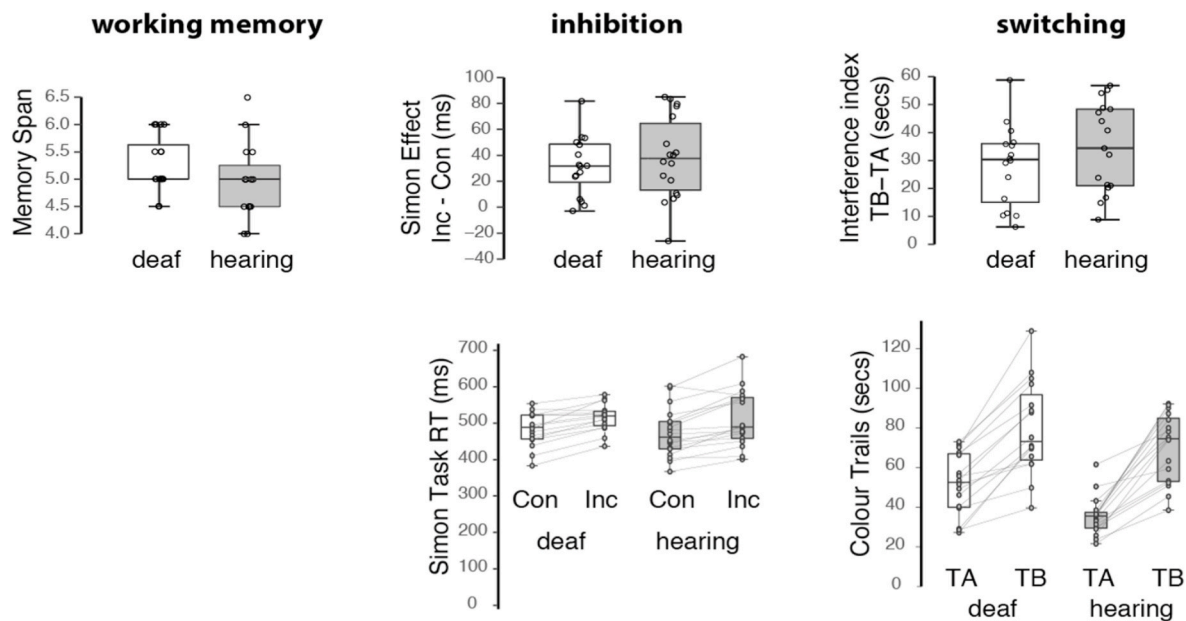
3. Results

3.1. Behavioural results

Results from the behavioural tests for both groups are shown in Fig. 1. A paired *t*-test showed no significant differences between groups in visual working memory span (t (29) = 1.6, p = .12), Simon effect (t (32) = 0.67, p = .51) and interference index (t (31) = 1.2, p = .23). There were no significant correlations between these covariates (Table 3).

3.2. Resting state fMRI results

Main effect of group: To identify differences between deaf and hearing individuals in ROI-to-ROI resting-state connectivity, we first used a 2nd level model with group as a between-subjects factor. Fig. 2 shows graphical displays of ROI-to-ROI resting-state connectivity, where 239 bivariate correlation coefficients were significantly different between groups (p < .05, FDR-corrected at seed level). Of those, the majority (221/239) of connections were between seeds in the auditory network and other brain networks, including somatomotor (A and B), salience/ventral attention (A and B), dorsal attention (A and B), DMN (A and B), limbic (A and B), control (B and C), visual (periphery) and language networks (Fig. 2B; Supp. Table 1). Most significantly, in the deaf group, there is a decrease in the strength of connectivity between the auditory network and bilateral somatosensory networks. There was also increased connectivity between the auditory and salience/ventral attention networks in the deaf group, mostly arising from auditory seeds in the right hemisphere (Fig. 2D).

When results from the behavioural tests were included as covariates in the 2nd level model, the general pattern of differences in connectivity between auditory-to-somatomotor and auditory-to-salience/ventral attention networks persisted, but the number of significantly different correlations was reduced to 154 (Fig. 2C; Supp. Table 2). Differences in connectivity between auditory and DMN, visual and language networks were no longer significant, suggesting that those differences are likely to be linked to inter-network connectivity mediating executive processing, and not driven by different sensory experience.

Effect of VWM covariate: The comparison of differences in correlations between resting-state connectivity and memory span in the VWM task revealed 28 significantly different bivariate correlation coefficients between groups (p < .05 FDR-corrected at seed/connection level; Fig. 3A; Supp. Table 3). As shown in Fig. 3B and C, differences are most frequently driven by connectivity results in the deaf group, with most of

Fig. 1. Behavioural results. The figure shows performance in all behavioural tasks in the hearing and deaf groups. The top panel shows the memory span (left), Simon effect (centre) and interference index (right), all of which were used as covariates in the resting-state analysis. The bottom panel shows the raw RT for each condition of the inhibition and switching tasks; these RTs were used to calculate the Simon effect and interference index (see Methods). Con: congruent; Inc: incongruent; TA and TB: A and B section of the colour trails task, respectively.

Table 3
Pearson correlations between behavioural covariates.

		Deaf	Hearing
VWM-Inhibition	Pearson's r	−0.293	−0.132
	p-value	0.271	0.640
VWM—Switching	Pearson's r	−0.392	−0.161
	p-value	0.134	0.567
Inhibition—Switching	Pearson's r	−0.091	0.263
	p-value	0.736	0.308

VWM: visual working memory.

the differences between groups arising from a seed in the left lateral occipital cortex (seed: ParOcc_1, x = −48 y = −66 z = 16). This seed is part of the dorsal attention A network in the classification of Schaeffer et al. (2018), but its coordinates coincide with the location of visual area MT/V5. In the auditory network, significant group differences included: 1) connections between the left Temp_Par_5 auditory seed (x = −58 y = −54 z = 10) and the left SPL_3 seed (x = −22 y = −66 z = 46) in the dorsal attention B network; 2) connections between the left Temp_Par_5 auditory seed and a seed in the left medial prefrontal cortex part of the DMN network A (PFCm_6, x = −6 y = 34 z = 20); 3) connections between right superior temporal cortex in the auditory network (seed: R_TempPAr_5, x = 50 y = −34 z = 2) and right extrastriate cortex in the visual central network (seed: ExStr_4, x = −16 y = −86 z = −16). It should be noted that in the deaf group, there are significant anti-correlations arising from adjacent posterior temporal and temporo-parietal seeds (Fig. 3D), most of which are part of the auditory and language network, and all of which are located in posterior temporal regions, where crossmodal plasticity effects are common in deaf individuals.

Effect of inhibition covariate: When evaluating the effect of performance in the inhibition task, group comparisons revealed significant differences in 39 bivariate correlation coefficients (p < .05 FDR-corrected at seed/connection level; Fig. 4; Supp. Table 4). Most differences (27/39) include a seed in the salience/ventral attention network A, the right precentral cortex R_PrC_1 seed (x = 52 y = 4 z = 40; see Fig. 4B). There are significant differences between groups in the

correlation between the inhibition covariate and the connectivity of the R_PrC1_ seed to.

● 20 medial frontal and parietal seeds of the DMN (A and B)
● 4 seeds in the left salience/ventral attention network A
● 1 seed in the auditory network (right superior temporal cortex), in the dorsal attention network A (right parietal cortex), and in the control B network (location).

Group differences in this analysis are driven mostly by results from the hearing group (Fig. 4D), where there is a negative correlation between the inhibition effect and internetwork connectivity between R_PrC1 in the salience/ventral attention networks (A and B) and seeds of the DMN networks (A, B and C). In other words, a smaller inhibition effect is linked to stronger connectivity between nodes in the salience and DMN network in the hearing group.

In the auditory networks, there were also significant group differences between the left temporo-parietal (LG TempPar_4 x = −52 y = −44 z = 4 and bilateral somatomotor cortex.

Effect of switching covariate: Group comparisons revealed 28 significantly different bivariate correlations between performance in the switching task and strength of connectivity (Fig. 5; Supp. Table 5). Of those, 10/28 were between seeds in the salience/ventral attention A and the DMN networks. 7/28 differences included connections between the Control C network and seeds in the DMN C, visual (periphery), Limbic A, Control A and somatomotor B networks. Most of these differences are driven by results in the hearing group, where there were significant correlations in the degree of interference in the colour trails task and the connection strength between several networks, including: salience, DMN, control, somatomotor, limbic A and visual. In particular, these were found between the salience A network and the DMN, and the salience A and control networks, and between the control C network and somatomotor network. In the deaf group, we did not observe these significant correlations between increased connectivity and a larger switching effect in these networks. Instead, we found largely negative correlations between connectivity and switching effect in most networks, including connections between auditory and somatomotor A and B, and auditory and salience/ventral attention A.

GROUP EFFECT (deaf > hearing)
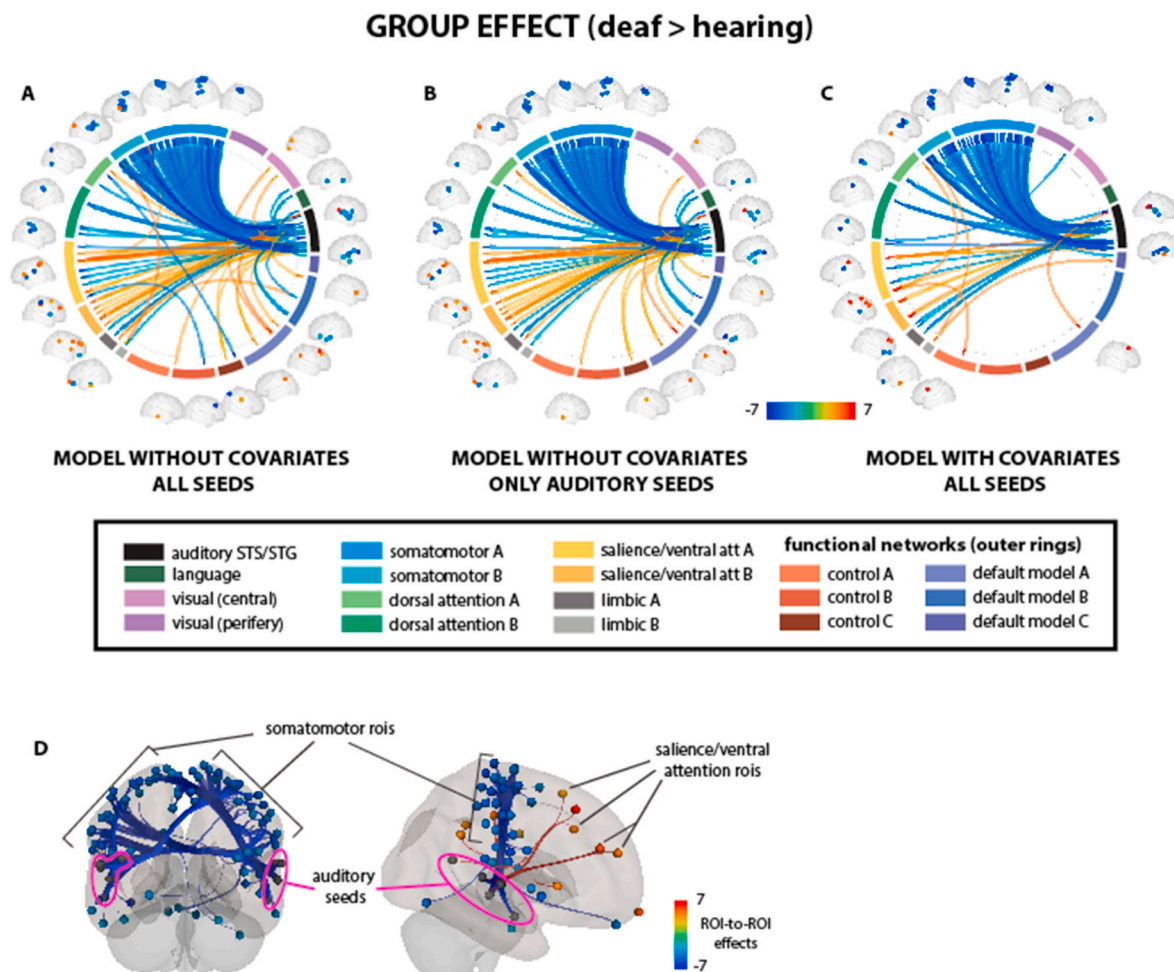
Fig. 2. Resting state connectivity differences between groups. A and B. Graphical display of ROI-to-ROI connectivity values for the contrasts [deaf > hearing] from a 2nd-level model with group as a between-subject factor. The wheels show results from all seeds (A) and only auditory seeds (B). C and D. Results for the contrast [deaf > hearing] in a 2nd-level model with group as between-subjects factors and results from the EF tests as covariates. C shows results from all seeds and D shows results from auditory seeds only. Auditory seeds in D are shown as grey-filled circles and enclosed by a pink line. Red/orange lines and circles indicate increased connectivity between ROIs in the deaf group; blue lines and circles indicate reduced connectivity strength in the deaf group.

4. Discussion

Here we investigated the influence of sensory experience in the organisation of resting-state networks of the brain and its relation to executive processing. Comparing resting-state connectivity between deaf and hearing individuals across 400 ROIs revealed differences in connectivity in 239 pairs of connections, most of which (221) included seeds in the auditory network. However, contrary to our prediction, when we investigated group differences in resting-state fMRI and their link to behavioural performance in executive function tasks (WM, inhibition and switching), we did not consistently find that EF performance correlated with the strength of connectivity between auditory and association networks. Instead, EF differences between groups were mostly linked to the salience and DMN networks. These findings suggest that sensory experience influences not only the organisation of sensory networks, but that it has also a measurable impact on the organisation of association networks.

4.1. Decreased connectivity between auditory and somatosensory networks in deaf individuals

Comparisons of whole-brain resting-state connectivity in deaf and hearing individuals showed reduced connectivity between auditory and somatomotor networks. These findings are in agreement with previous studies of resting-state connectivity in deaf individuals (Bonna et al., 2021; Andin and Holmer, 2022). This could be due to stronger synchronisation between auditory and somatomotor areas in hearing individuals, linked to feedforward and feedback loops subserving speech production and perception (Hickok et al., 2009; Price et al., 2011). Such synchronisation will be reduced in deaf individuals, for whom language relies strongly on visual information.

Another possibility is that this finding reflects general connectivity changes of typically considered 'sensory' regions in the absence of their main sensory input. Similar patterns of reduced connectivity between a deprived sensory area and other sensory regions are also observed in blind individuals (Bonna et al., 2021; Burton et al., 2014; Guerreiro et al., 2021; Kanjlia et al., 2021; Liu et al., 2007; Pelland et al., 2017; Yu et al., 2008). This suggests that our finding could also reflect a common mechanism or functional organisational principle of sensory experience driving the connectivity between 'sensory areas' (Bedny, 2017; Cardin et al., 2020; Collignon et al., 2013; Röder and Kekunnaya, 2021). A different sensory experience could result in a different function for those sensory areas and a different developmental pathway. This is supported by findings of neural functional organisation in deaf individuals reminiscent of the organisation found in the developing brain of infants during higher-order cognitive tasks. For example, occipital and temporal regions are recruited during switching tasks in children (Engelhardt et al., 2019), whereas these same regions are typically involved in visual

Effect of Visuo-spatial Working Memory Covariate
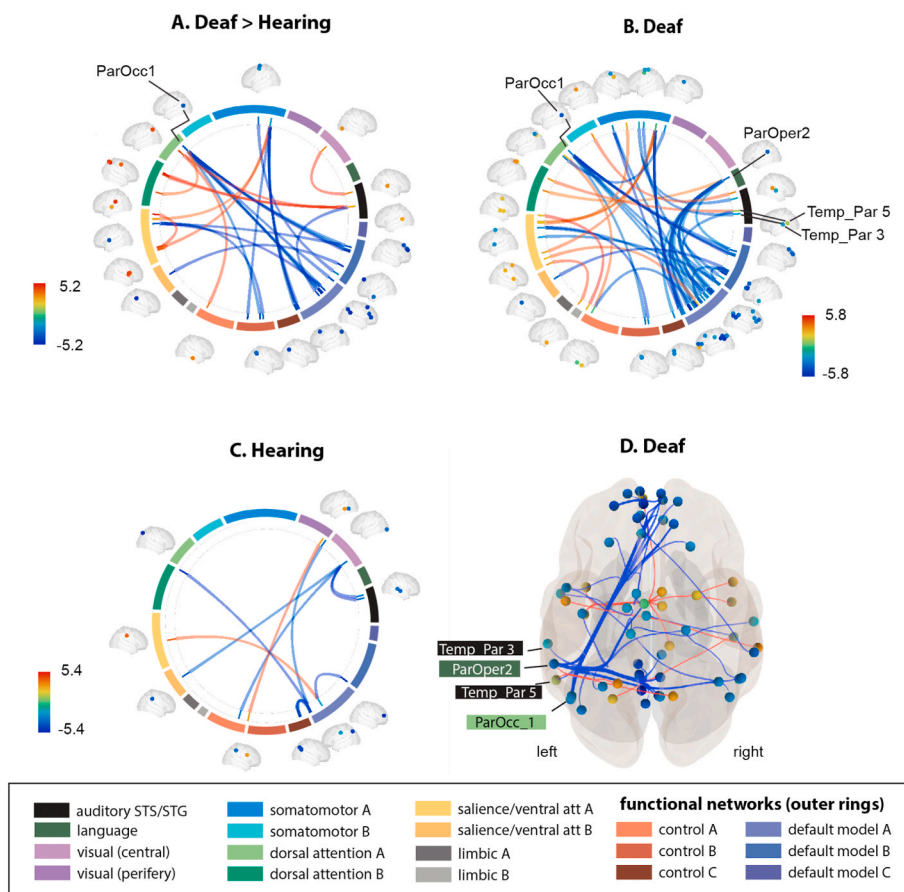
Fig. 3. Effect of visuo-spatial working memory covariate (VWMcov) on resting-state connectivity in the deaf and hearing groups. A. Results for the contrast [VWMcov deaf > VWMcov hearing]. **B.** Results of the VWMcov in the deaf group. **C.** Results of the VWMcov in the hearing group. **D.** Top view of the brain with overlapped connectivity results for the VWMcov in the deaf group. ParOcc_1: left parieto-occipital_1, x = −48 y = −66 z = 16. Temp_Par_5: left temporo-parietal 5, x = −58 y = −54 z = 10. ParOper_2: left parietal operculum 2, x = −58 y = −44 z = 28. Temp_Par 3: left temporo-parietal 3, x = −62 y = −32 z = 6.

and auditory processing in sensory-typical adults. However, temporal regions of deaf adults are also recruited during a switching task (Manini et al., 2022), suggesting that auditory inputs could displace functions such as switching from the superior temporal cortex. This should not be interpreted as reflecting lesser maturation or presence of a deficit, given that deaf (and blind) adults perform at similar levels to hearing and sighted adults in such tasks (provided that delayed language development is not a confound). Rather, it suggests that environmental experience can modulate the specialisation of sensory cortices, both for sensory and cognitive processing. Further research on the developing brain of deaf and hearing individuals is necessary to test this hypothesis.

Functional connectivity between sensory areas also varies with task demands. In sighted individuals, there is higher synchronisation between sensory areas during rest than during a task; the opposite pattern of activity is found in blind individuals (Pelland et al., 2017). However, the caveat is that these are examples of connectivity at rest vs. connectivity during unimodal tasks. Stimuli and tasks using coherent multisensory information show increased synchronisation of activity across sensory areas (Herbec et al., 2015; Sonkusare et al., 2019). Also, synchronisation of activity between visual areas and other sensory regions during rest is higher when participants have their eyes closed than when they have their eyes open (Guerreiro et al., 2021). This difference between eyes open and closed is not found in blind individuals, where differences between sighted and blind individuals in the synchronisation between visual and non-visual areas are only found in the eyes closed condition (Guerreiro et al., 2021).

## 4.2. Increased connectivity between auditory and salience networks in deaf individuals

We found increased connectivity between auditory seeds and right PFC seeds of the salience networks in the deaf group. Typical crossmodal plasticity effects, such as higher activations during a visual task in deaf compared to hearing individuals, have been found in the right superior temporal cortex under several experimental conditions, including different sensory modalities (visual, somatosensory) and different tasks (working memory, attention, discrimination, detection) (Fine et al., 2005; Karns et al., 2012; Ding et al., 2015; Benetti et al., 2017, 2021; Bola et al., 2017; Cardin et al., 2018; Manini et al., 2022; Zimmermann et al., 2021). This ubiquity suggests a role of this region in multisensory or higher-order processes, such as attention or control (Cardin et al., 2020). In a previous study, we found that deaf auditory areas are activated during task switching, but not during other cognitive tasks, suggesting a role in attention reallocation or shifting, rather than control (Manini et al., 2022). The increased connectivity between the right auditory cortex and seeds of the salience/ventral attention networks supports this finding, as it has been reported that the salience/ventral attention network is involved in reallocation of attention to task-relevant events and shifting of attention between task sets (Corbetta et al., 2008; Uddin, 2015). The involvement of the deaf auditory cortex in such functions could be due to its proximity to TPJ, a core component of this network, or due to functional specialisation for switching (see discussion above). These findings are also consistent with findings from studies in blind individuals, which have shown increased resting-state connectivity between visual regions and cortical areas which are part

Effect of inhibition covariate
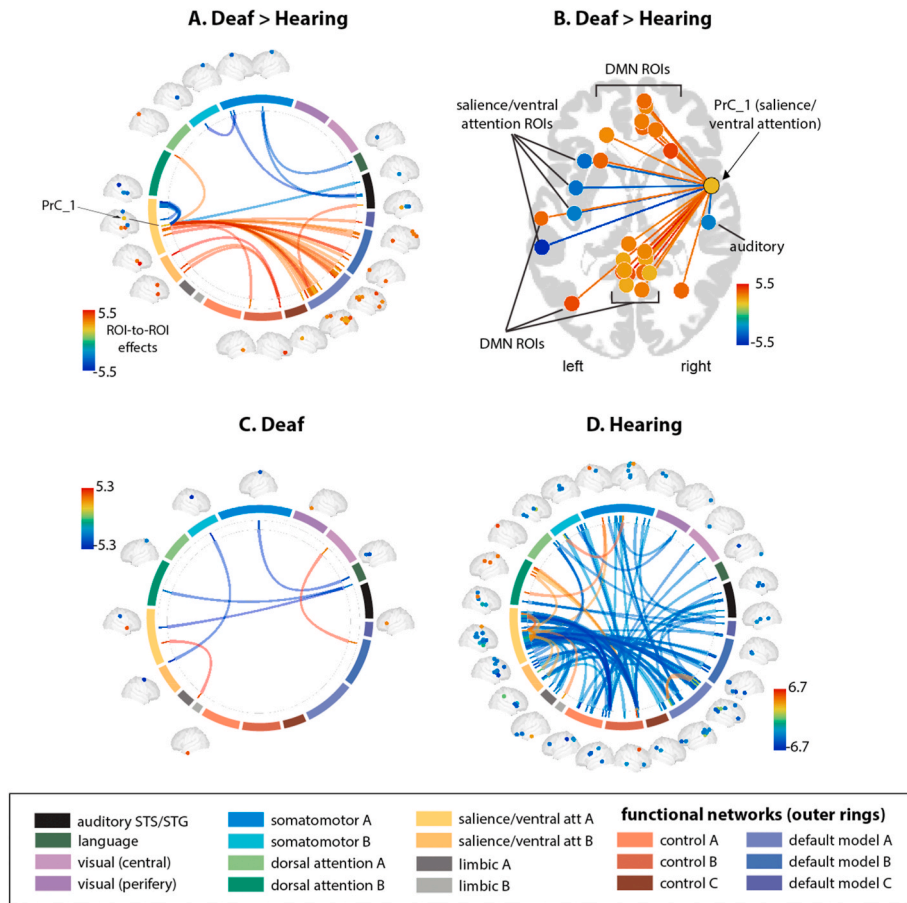
Fig. 4. Effect of inhibition covariate on resting-state connectivity in the deaf and hearing groups. A. Results for the contrast [Inhibition_covariate deaf > Inhibition_covariate hearing]. **B.** Connectivity differences between groups arising from the seed PrC_1: right precentral 1, x = 52 y = 4 z = 40. **C-D.** Results of the inhibition covariate in the deaf (C) and hearing (D) groups separately. DMN: Default Mode Network.
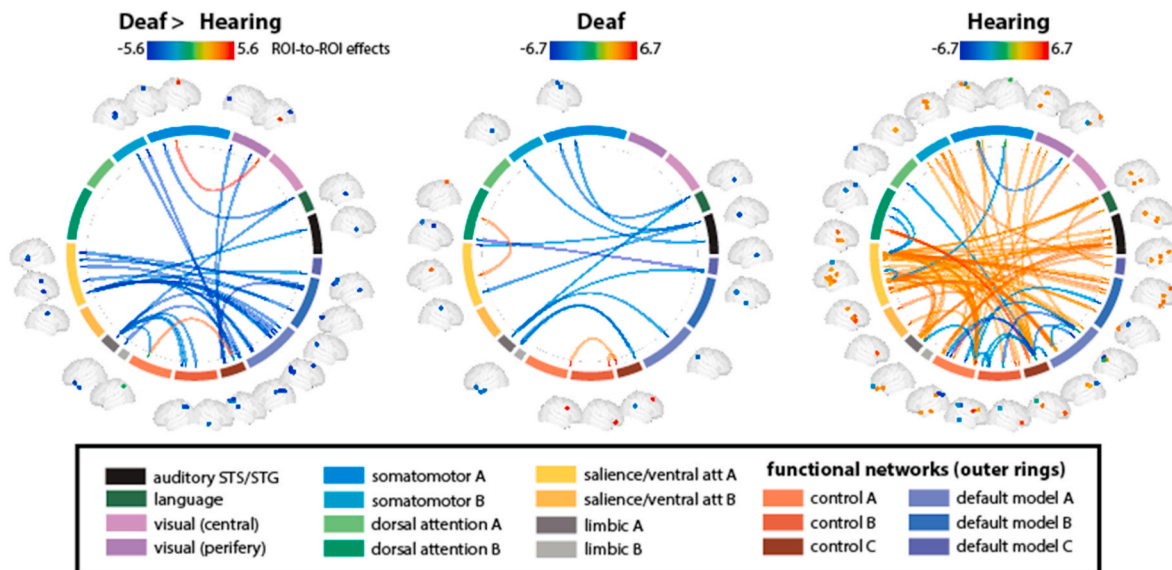
Fig. 5. Effect of switching covariate (switch_cov). **A.** Results for the contrast [switch_cov deaf > switch_cov hearing]. **B–C.** Results of the switch_cov in the deaf (C) and hearing (D) groups separately.

of the salience network, such as the right middle frontal gyrus (Burton et al., 2014), suggesting again a common mechanism for reorganisation of sensory regions in the absence of their main sensory input.

4.3. Sensory experience modulates the reorganisation of networks involved in EF processing

Group comparisons also showed differences in resting-state connectivity between the auditory network and the DMN, visual, control and language networks. However, these differences were no longer significant when executive function covariates were included in the 2nd level model. Thus, such findings are more likely to be associated with inter-network connectivity mediating executive processing. In fact, when evaluating the link between EF covariates and resting-state connectivity in both our groups, significant differences were mostly found in the salience/ventral attention and DMN networks, rather than in the auditory network. These findings suggest that sensory experience influences not only the organisation of sensory regions of the brain, but also the organisation of networks involved in cognitive processing.

Our results show significantly different associations between resting connectivity and EF in each group, suggesting that even when performance in EF tasks is similar, each group may rely on different neural substrates to achieve this. In the VWM task, differences in correlations between resting-state activity and performance in the task were mainly driven by findings from the deaf group. In this group, many of the significant correlations with performance in the VWM task arise from seeds in the left posterior temporal cortex and temporo-parietal junction. These brain regions are involved in speech and language processing in hearing individuals, and in sign language and speechreading processing in deaf individuals (Capek et al., 2008; Cardin et al., 2013; Emmorey et al., 2011, 2014; Leonard et al., 2012; Que et al., 2018; Twomey et al., 2017). In the group comparisons, the seed with most differences corresponded to left ParOcc_1 seed (x = −48 y = −66 z = 16), where area MT/V5 is located. Activation of visual-motion sensitive cortex MT/V5 has been shown during sign language processing in both deaf and hearing signers (Capek et al., 2010; McCullough et al., 2012)). It is known that language modality and sensory experience influence strategies and coding during working memory tasks (Wilson et al., 1997; Wilson and Emmorey, 1997) and that deaf signers use sign language-based coding in visual working memory tasks (MacSweeney et al., 1996). Our findings of anticorrelation between connectivity strength and VWM span suggest that deaf signers might be able to rely more on their experience of visual language to solve the Corsi VWM task, and that the connectivity of areas involved in visual language processing can be predictive of performance.

In the switching task, we found that stronger correlations between the salience and DMN networks are linked to an increased interference index in the hearing group. This is in agreement with literature proposing a role of the salience network, and in particular the anterior insula, in shifting between attentional states, and directing other brain networks, such as DMN and control, towards stimuli or tasks for further or preferential cognitive processing (Menon and Uddin, 2010; Sridharan et al., 2008). It has been shown that anticorrelation between salience and DMN is linked to successful cognitive effort (Putcha et al., 2016). Specifically, anticorrelation between the salience and DMN during resting-state predicted better switching in a Trails making task, both in Parkinson's patients and control participants (Putcha et al., 2016). Notably, in our study, this relationship was not found in the group of deaf individuals, resulting in significant differences between hearing and deaf groups. Results from the inhibition task also showed significant differences between groups. These mostly involved connections between seeds in the right PFC (salience network) and seeds in the DMN, and to a lesser extent, other seeds in the salience, control, and auditory networks. Again, most of these differences were driven by significant correlations in the hearing group, where the inter-network connectivity of the salience network, including PFC seeds, was anticorrelated with the size

of the inhibition effect. These results from the hearing group agree with the wider literature from neurotypical individuals, where it is known that the rIFC is important for inhibitory control, and its activation predicts individual differences in inhibitory control abilities (Aron et al., 2014; Cai et al., 2014). However, as with the switching task, such correlations between performance and resting state connectivity were not found in the deaf group, perhaps because this kind of process in deaf individuals involves a modified network organisation, with the salience/ventral attention network incorporating components of the auditory cortex. Overall, these results suggest that the organisation of networks for EF processing is modulated by sensory experience.

The fact that we find striking significant differences between deaf and hearing individuals, and the observation that the results from hearing individuals are in agreement with what is generally found in the broader literature of inhibition and switching, highlight that our understanding of brain function based on studies of the hearing brain cannot be directly extrapolated to the deaf brain. Although deaf and hearing individuals perform similarly in these tasks, their performance is likely to be bound to different neural organisation and function. It should also be noted that the predefined brain parcellation we used to compare connectivity of the same anatomical regions in both groups was constructed using data from hearing, neurotypical individuals. Similarly, even though we used visuo-spatial tasks suitable for both deaf and hearing individuals, these tasks were also created and standardised for hearing individuals. It is therefore not surprising that results from the hearing group are in agreement with the broader literature of connectivity and EF, and highlight the need to incorporate data from special populations for a full understanding of brain function.

It should be kept in mind that deaf and hearing individuals do not only differ in their sensory experience, but also in their social and cultural experiences. These differences could also be behind some of the connectivity differences. Greene et al. (2022) showed that the relationships between brain measurements and phenotypes reveal composite experiences. In other words, they reveal interactions between attributes in a group, where most of those attributes are kept constant. For example, race, education, and socio-economic status tend to be constant in groups tested in many psychology and neuroscience studies, and these interact with the variables of interest. In our study, results from each of our groups are also likely to reflect a composite of their experiences, not only sensory processing. In support of this, Sen et al. (2022) found more variability in connectivity patterns in blind individuals, and that these differences between blind and sighted individuals could be explained by differences in educational background. Group differences could also reflect different mental states and compliance with the instructions, which are difficult to measure in resting state studies, but nevertheless can impact connectivity patterns (Buckner et al., 2013).

Greene et al. (2022) also found that deviation by an individual from the group stereotype, cannot be predicted with typical brain-phenotype models. This agrees with our findings in this study, where we observe that the relationship between EF performance and brain connectivity for the group of sensory-typical individuals falls well with what is known in the literature of resting state connectivity and EF. However, when sensory experience results in a misalignment with the commonly tested stereotypic group, as in the case of deaf individuals, these relationships do not hold.

5. Limitations

One of the advantages of resting state fMRI is that it can provide functional connectivity maps without the constraints of a specific task. However, it is important to keep in mind the limitations of this approach, especially when making inferences about its relationship to behavioural outcomes. It is often assumed that resting state connectivity fMRI reflects permanent organisational relationships in the brain. However, it has been argued that resting state is also an arbitrary task

state, associated with its own biases as much as any other task (Buckner et al., 2013). This argument is supported by evidence showing connectivity differences between resting state scans with eyes open and eyes closed (Patriat et al., 2013; Guerreiro et al., 2021). Additionally, several studies suggest that connectivity studies of naturalistic stimuli or task-fMRI are better predictors of behavioural differences than those of resting state fMRI (Finn et al., 2017; Greene et al., 2018; Zhao et al., 2023). This is because specific tasks engage activity in networks linked to the behaviour of interest, enhancing associations between brain activity and different traits (Finn et al., 2017). In the present study, we found significantly different associations between resting connectivity and EF parameters in deaf and hearing individuals. This suggests that different network dynamics might be implemented by each group. However, given the explained limitations, this remains a working hypothesis until it can be directly tested with specific task-fMRI targeting the executive components of interest.

Another limitation of our study is that the cause of deafness is likely to be different across participants. Here, we wanted to investigate how a common experience, that of having a reduced access to sound early in life, shaped brain connectivity. This is a common experience to all participants in our study, independently of the cause of deafness, and indeed all participants identified as part of the same cultural group. While disentangling any potential effects of cause of deafness is beyond the possibilities and scope of this study, it is still an open question of how different causes of deafness shape brain structure and function, including the very early auditory experience of those who lose their hearing early in infancy vs those who are congenitally deaf. Further studies are necessary to address this question.

6. Conclusion

The study of EF processing in deaf and hearing individuals has shown commonalities in the neural substrates subserving these processes, but also important differences, which suggest that environmental experience modulates the organisation of cognitive networks (Cardin et al., 2018; Ding et al., 2015; Manini et al., 2022). Our findings in this study support this notion. We found in the deaf group significantly increased resting-state connectivity between the salience and auditory networks, and decreased connectivity between auditory and somatomotor networks compared to the hearing group. There were also striking differences between groups in the correlation between EF measurements and resting-state connectivity, mainly involving the salience and DMN networks. These findings suggest that sensory experience impacts the organisation of EF networks in the adult brain, and that EF processing in the adult brain can be achieved through different brain developmental pathways and functional organisation.

Credit author statement

VC, EK, AK, TD, KI and BW designed the study. EK, AK, VV and TD collected the data. VC, VV, EZ and PK analysed the data. VC and BW wrote the paper.

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108583.

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