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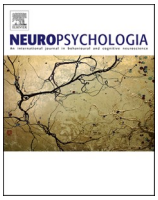

Reorganization of large-scale brain networks in deaf signing adults: The role of auditory cortex in functional reorganization following deafness

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ABSTRACT

If the brain is deprived of input from one or more senses during development, functional and structural reorganization of the deprived regions takes place. However, little is known about how sensory deprivation affects large-scale brain networks. In the present study, we use data-driven independent component analysis (ICA) to characterize large-scale brain networks in 15 deaf early signers and 24 hearing non-signers based on resting-state functional MRI data. We found differences between the groups in independent components representing the left lateralized control network, the default network, the ventral somatomotor network, and the attention network. In addition, we showed stronger functional connectivity for deaf compared to hearing individuals from the middle and superior temporal cortices to the cingulate cortex, insular cortex, cuneus and precuneus, supramarginal gyrus, supplementary motor area, and cerebellum crus 1, and stronger connectivity for hearing non-signers to hippocampus, middle and superior frontal gyri, pre- and postcentral gyri, and cerebellum crus 8. These results show that deafness induces large-scale network reorganization, with the middle/superior temporal cortex as a central node of plasticity. Cross-modal reorganization may be associated with behavioral adaptations to the environment, including superior ability in some visual functions such as visual working memory and visual attention, in deaf signers.

1. Introduction

Cortical areas that are deprived of sensory input during development reorganize to respond to the preserved senses (Bavelier and Neville, 2002; Merabet and Pascual-Leone, 2010). Thus, individuals who are deprived of sensory input in one modality, due to e.g., deafness or blindness, hold an important clue to understanding brain reorganization. Early deafness has repeatedly been associated with reorganization of the auditory cortex (Cardin et al., 2018; Emmorey et al., 2011; Karns et al., 2012; Malaia et al., 2014), but there is also some evidence of reorganization beyond this region (Bonna et al., 2020; Li et al., 2016). In the present study, we apply a data-driven approach, i.e., independent component analysis (ICA) on resting-state fMRI data, to further our understanding of how network organization differs between deaf and hearing individuals. This will in turn have implications for how findings from functional connectivity studies that investigate network nodes can be interpreted. The focus of this study is on an adult deaf population for whom sign language learning has been optimized by early sign language interventions and bilingual schooling with sign language as the main mode of communication (Bagga-Gupta, 2004; Meristo et al., 2007). The combination of fluent language skills and lack of auditory input makes deaf signers a highly valuable study population for investigating cortical reorganization due to sensory deprivation. However, with the introduction of cochlear implants in almost every deaf infant in the Western world, including Sweden where this study is situated, the current cohort is likely to represent one of the last cohorts of its kind.

The lack of sensory input induces changes in brain regions associated with the processing of the remaining senses, as well as in the region typically used for processing the sense that is lost. These changes are associated with behavioral adaptations, and sometimes even superior skills compared to individuals with no sensory impairment (for a review see Merabet and Pascual-Leone, 2010). For example, the lack of visual input in blind individuals is associated with recruitment of the visual cortex, i.e., the sensory-deprived area, for tactile Braille reading (Reich et al., 2011), sound localization (Gougoux et al., 2005), and verbal processing (Amedi et al., 2004). Superior processing of auditory stimuli has further been associated with altered processing in areas of the remaining senses, i.e., in the superior temporal cortex (Stevens and

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Weaver, 2009). Similarly, deaf individuals recruit the sensory-deprived area, auditory cortex, for visual (Andin et al., 2021; Bottari et al., 2014; Cardin et al., 2013; Emmorey et al., 2011; Karns et al., 2012) and vibrotactile perception (Auer et al., 2007; Karns et al., 2012), as well as cognitive tasks (Andin et al., 2021; Cardin et al., 2013, 2018; Ding et al., 2015; Twomey et al., 2017). These neural changes may also be related to superior behavioral performances in for example visual attention (for an overview, see Bavelier et al., 2006; MacSweeney and Cardin, 2015). However, few studies have investigated the recruitment of areas of the remaining senses for deaf individuals, e.g., visual cortex.

Brain imaging studies have typically investigated task-based differences in distinct, pre-defined regions, primarily in the superior temporal cortex. However, the brain is organized in large-scale brain networks where several brain regions communicate and work in sync with each other, both during specific tasks and during rest (e.g., Petersen and Sporns, 2015; Thomas Yeo et al., 2011). To understand the role of a specific region, it is necessary to investigate inter-regional associations at a network level (Uddin et al., 2019). There is no consensus on network taxonomy, but Uddin et al. (2019) recently proposed a six-network solution as a universal taxonomy of large scale brain networks. The six networks were given anatomical names and include the occipital network, the pericentral network, the dorsal frontoparietal network, the lateral frontoparietal network, the midcingulo-insular network, and the medial frontoparietal network. Each network was further connected to a cognitive domain and to core regions, outlined in Table 1 together with main behavioral functions connected to each network. In the present paper, we primarily refer to the networks based on their cognitive domain.

To understand how large-scale networks are organized, functional connectivity analysis is used. This is typically done by investigation of functional connectivity between regions of interest (ROI-to-ROI analysis) or from a seed to all voxels in the brain (seed-to-voxel analysis). Several studies have explored functional connectivity between superior temporal regions and other brain regions in deaf individuals. For example, we recently showed enhanced functional connectivity from the auditory cortex to several brain regions, primarily in the visual cortex, for deaf signers compared to hearing non-signers during a visual working memory task (Andin et al., 2021). Bola et al. (2017) also found stronger functional connectivity between auditory and visual cortices for deaf individuals when administering a rhythm discrimination task in the visual modality. During rest, studies have shown stronger connectivity for deaf compared to hearing individuals between superior temporal cortex and posterior cingulate, precuneus and the intraparietal lobule (Malaia et al., 2014), anterior cingulate cortex (Ding et al., 2016), insula (Ding et al., 2016; Striem-Amit et al., 2016), calcarine sulcus (Shiell et al., 2014), visual (Benetti et al., 2021) and frontal regions (Cardin et al., 2018; Ding et al., 2016). However, weaker functional connectivity between temporal regions and the visual word form area (Wang et al., 2015) and somatomotor areas (Bonna et al., 2020) has also been demonstrated. Several auditory and visual brain regions have further been shown to be structurally connected in both deaf and hearing individuals (Li et al., 2015). However, Shiell et al. (2014) suggested that the connection between auditory and visual regions is enhanced during visual processing due to the lack of auditory processing in deaf populations. Although most studies have focused on the superior temporal cortices, some studies have found reorganization beyond these regions. Connectivity from visual cortices has been found to be stronger for deaf compared to hearing individuals to frontoparietal areas (Bonna et al., 2020; Dell Ducas et al., 2021), the default network, and the salience network (Dell Ducas et al., 2021), and weaker to the language regions, both functionally (Li et al., 2016) and structurally (Dell Ducas et al., 2021; Li et al., 2015). Li et al. (2016) investigated functional connectivity from the limbic system and found stronger connectivity to both visual and language processing regions for deaf, compared to hearing, individuals. Reorganization has further been confirmed by morphological changes in deaf individuals for the occipital cortex (Allen et al., 2013; Pénicaud et al., 2012) and in temporal regions (Hribar et al., 2014; Kumar and Mishra, 2018; Shibata, 2007).

ICA has been used to characterize large-scale brain networks in, and between, different populations. While seed- and ROI-based functional connectivity analyses are appropriate when the purpose is to describe group differences in connectivity pattern for the pre-selected seeds, these analyses do not reveal whether group differences exist in the underlying network structures. To investigate network separation, ICA can be used instead. Wang et al. (2014) applied ICA to compare congenital blind and sighted individuals and found differences between groups in the visual network, which is mainly involved in the processing of visual stimuli, and in the salience network, which is engaged for attention switching to salient stimuli. Dell Ducas et al. (2021) used ICA to identify difference between deaf and hearing individuals in the spatial extent of regions within the default network. Further, for deaf compared to hearing cats, Stolzberg et al. (2018) showed patterns of altered functional connectivity in networks including auditory, visual, cingulate, and somatosensory regions. However, to the best of our knowledge, no previous study used ICA to fully characterize large-scale networks in deaf signing individuals, which can further our understanding of plasticity due to deafness and sign language use. In the present study, we use data-driven ICA aiming to characterize group differences in resting-state functional connectivity between deaf signers and hearing non-signers in the organization of large-scale brain networks.

2. Materials and method

2.1. Participants

Fifteen deaf early signers (eight female) and twenty-four hearing non-signers (twelve female) were included in the study. There were no significant group differences for gender distribution, non-verbal cognitive ability (tested using the Visual puzzles subtest from Weschler Adult Intelligence Scale), or level of education. However, there was a group difference in age with the deaf signers ($M = 35.0$, $SD = 7.8$) being significantly older than hearing non-signers ($M = 26.5$, $SD = 7.5$), $t(37)$

Table 1
Overview over large-scale brain networks, based on Uddin et al. (2019).

Anatomical name	Cognitive domain	Core regions	Main behavioral functions
Occipital network	Visual	Occipital lobe	Visual processing
Pericentral network	Somatomotor	Motor cortex, somatosensory cortex	Motor processing, somatosensory processing
Dorsal frontoparietal network	Attention	Superior parietal lobule, intraparietal sulcus, middle temporal complex, frontal eye field	Visuospatial attention; top-down processing of stimuli and responses
Lateral frontoparietal network	Control	Lateral prefrontal cortex, middle frontal gyrus, anterior inferior parietal lobule, intraparietal sulcus	Executive functions; goal-oriented cognition, working memory, inhibition, switching
Midcingulo-insular network	Salience	Anterior insula, anterior midcinulate cortex	Detection of salient information
Medial frontoparietal network	Default	Medial prefrontal cortex, posterior cingulate cortex, posterior inferior parietal lobule	Goal directed cognitvion, monitoring the environment, processing of associative representations, elaboration of events etc

= 3.4, $p = 0.002$. Inclusion criteria were normal or corrected-to-normal vision, right-handedness, and normal or above normal non-verbal cognitive ability. Exclusion criteria included claustrophobia, pregnancy, and having non-MR compatible implants. Nine of the participants had their deafness discovered at birth, while the remaining six were between 6 month and 3 years when their deafness was discovered. All deaf signers were considered early signers, using Swedish Sign Language (*Svenskt Teckenspråk*; STS) as their primary language, performing on par with an independent sample of deaf native signers on the STS sentence repetition test (Schönström and Hauser, 2021). Five participants were signed with from birth and nine reported starting acquisition of STS before the age of three. For one participant, age of acquisition was missing. None of the participants relied on hearing aids for verbal communication, although two participants used hearing aids for sound awareness. The hearing participants were native Swedish speakers without any knowledge of STS. The study was approved by the regional ethical review board in Linköping (Dnr, 2016/344–31) and was conducted in accordance with the Declaration of Helsinki. Participants gave their written informed consent and were compensated for their participation.

2.2. Image acquisition

Structural and functional MRI data were collected with a Siemens Magnetom Prisma 3T scanner (Siemens Healthcare, GmbH) at the Center for Medical Image Science and Visualization (Linköping University, Sweden) using a 64-channel head coil. The scanning started with acquisition of structural images using a T1-weighted three-dimensional magnetization-prepared rapid gradient echo (MPRAGE) sequence with the following parameters: FOV = 288 × 288, acquisition matrix = 208 × 288 × 288, voxel size = 0.90 × 0.86 × 0.86 mm, TR = 2300 ms, TE = 2.36 ms, TI = 900 ms, FA = 8°. Resting-state data was acquired at the end of the scanning after the participants had performed four task-EPI runs (Andin et al., 2021), using a BOLD multi-plex EPI sequence during a 10-min scan with the following parameters: FOV = 192 × 192 mm, voxel size = 3 × 3 × 3 mm, TR = 1340 ms, TE = 30 ms, FA = 69°, number of slices = 48, 440 vol, interleaved/simultaneous acquisition.

2.3. Data processing

Preprocessing was performed using the default pipeline in CONN functional connectivity toolbox (Version 20.b; www.nitric.org/projects/conn, RRID: SCR_009550) running under Matlab R2018a (The MathWorks Inc., Natick, MA). The preprocessing steps included functional realignment, unwarping and co-registration to the first scan, slice-timing correction to adjust for temporal misalignment between slices, outlier detection by computation of framewise displacement (outliers defined as displacement >0.9 mm or BOLD signal change >5 *SD*.), normalization into standard MNI space, structural segmentation into grey matter, white matter and CSF tissue classes, and smoothing using a Gaussian kernel of 8 mm full width half maximum to increase signal-to-noise ratio. The realignment parameters and the noise components from the outlier detection were used as first-level covariates. Linear regression using the anatomical component-based noise correction (aCompCor) algorithm was implemented to remove effect from subject specific physiological noise such as white matter and cerebrospinal areas, motion parameters, outlier scans (scrubbing) and session-related slow trends. Quality assurance checks showed that there were no group differences in number of scrubbed slices, max motion, or global signal change. However, the deaf group had significantly higher mean motion, i.e., the absolute displacement of each brain volume compared to the previous estimated from the x, y and z translation parameters (DS: $M = 0.15$, $SD = 0.05$; HN: $M = 0.12$, $SD = 0.04$; $t(37) = 2.4$, $p = 0.023$), why this parameter was included as a covariate in all group analyses. Second-level covariates thus included group (deaf early signers/hearing non-signers), age (mean-centered), and the mean motion parameter from the realignment step. Denoising included linear regression of potential confounding effects and temporal processing using bandpass filtering (0.008, 0.09 Hz).

To identify networks that are functionally connected, independent component analysis (ICA) was performed by estimating spatially independent patterns in the fMRI data. Independent components across both groups were determined using a G1 FastICA algorithm for component definition at the group-level and GICA 3 subject-level back projection. Dimensionality reduction was set to 64. ICA was performed with the number of components set to eight, sixteen, twenty-four, and thirty-two. Each analysis was visually inspected and matched to the six networks described by Uddin et al. (2019), and automatically to the network templates included in CONN. The twenty-four-component setting rendered the best overall solution. Nine of the twenty-four components matched the large scale brain networks by Uddin et al. (2019) and were included in further analyses (Fig. 1). Generally, a lower number of components (around 20) are used when the aim is to identify functional large-scale networks, as in the present study, while larger number of components (above 100) are used for brain parcellation (Ray et al., 2013).

2.4. Data analysis

To identify group-differences in the nine independent components, the spatial maps of each component were analyzed using between-subjects contrasts with age and mean motion as covariate (1, −1, 0, 0). Results were voxel thresholded at $p < 0.001$ uncorrected, and cluster thresholded at $p < 0.05$ using False Discovery Rate to control for type 1 errors. For independent components with significant differences between groups, the significant clusters were exported and used as seeds in seed-to-voxel analyses. Group differences in functional connectivity were investigated using the same contrasts and the same thresholding as for the ICA. Further, functional connectivity measures and effect size (beta values) of each significant cluster were extracted.

3. Results

3.1. Independent component analysis

The nine independent components that best matched the six networks proposed by Uddin et al. (2019) are presented in Fig. 1. For three networks, two separate components were chosen since they represented typical sub-networks. Thus, the visual network (occipital) was represented by a medial and a lateral component (Fig. 1a and b), the somatomotor network (pericentral) was represented by a ventral and a dorsal component (Fig. 1c and d), and the control network (lateral frontoparietal) by a left and a right component (Fig. 1e and f). The attention network (dorsal frontoparietal), salience network (the midcingulo-insular), and the default network (medial frontoparietal) were best captured by one single component each (Fig. 1g–i). Group differences, with stronger connectivity for deaf signers compared to hearing non-signers, were found in the default network component. Stronger connectivity for hearing non-signers compared to deaf signers were found in the ventral somatomotor network, the left control network, and the attention network (Fig. 2). The four independent components in which group differences were identified match different large-scale networks. However, all significant clusters in the between-group analysis except one were found in the superior and middle temporal regions. For the default network component, peak voxels were found in the left temporal pole, right superior and left middle temporal gyri. For the component representing the left control network, peak voxels were found in bilateral superior temporal gyrus and right pallidum. The ventral somatomotor network component showed peak voxels in left superior temporal gyrus, while the component representing the attention network had peak voxels in right superior temporal gyrus (Table 2).

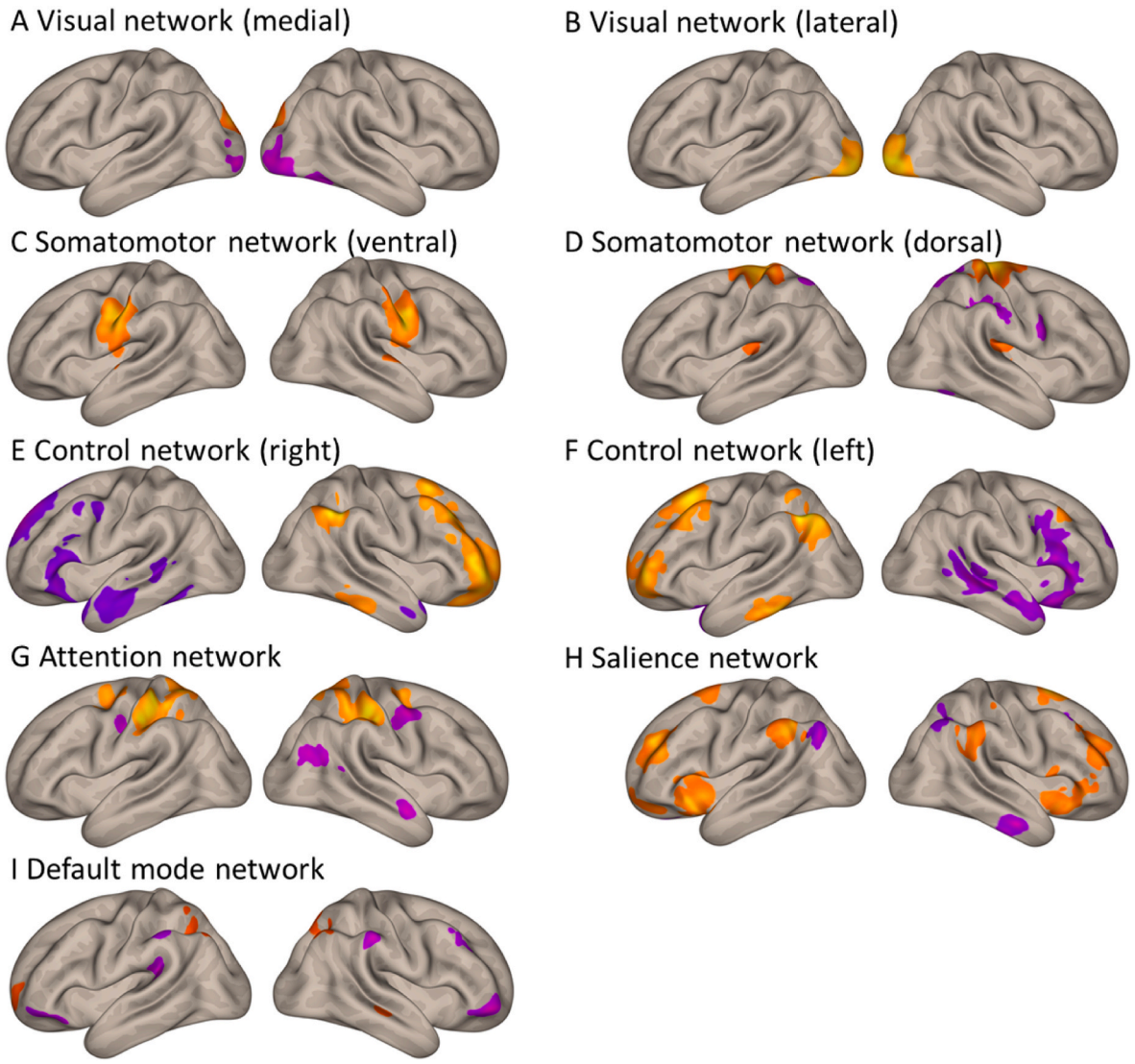


Fig. 1. Large-scale brain networks identified in the independent component analysis. The visual network (occipital network) divided into A) medial part and B) lateral part. The somatomotor network (pericentral network) divided into C) ventral part and D) dorsal part. The control network (lateral frontoparietal network) divided into E) right part and F) left part. G) Attention network (dorsal frontoparietal network), H) salience network (midcingulo-insular network), and I) default network (medial frontoparietal network). Yellow represents regions positively correlated within the network, and purple represents regions negatively correlated. Brighter color represents stronger correlation.

3.2. Seed-to-voxel analysis

We localized group differences in temporal regions and the right palladium (Table 2). To further investigate how these regions might differ in connectivity across groups, we used the clusters ($n = 8$) as masks in subsequent exploratory seed-to-voxel analysis. Group, age, and the mean motion parameter were used as second-level covariates. The seed regions overlapped with each other and the resulting connectivity maps showed considerable similarities (Fig. 3A-E). The seed in right pallidum resulted in no significant connections and is therefore not included in the figure. Deaf signers showed stronger connectivity between the temporal seeds and targets in the cingulate cortex, insular cortex, superior temporal cortex, cuneus and precuneus, supramarginal gyrus, supplementary motor area, and cerebellum crus 1. Hearing non-signers showed stronger connectivity to clusters including hippocampus, middle/superior frontal gyrus, pre- and postcentral gyrus, and cerebellum crus 8. Details of connectivity measures are provided in Table S1.

4. Discussion

We sought to investigate large-scale brain networks in deaf signers, and how these differ from hearing non-signers. Our findings confirm that temporal regions are subject to cross-modal reorganization in deaf individuals. For the nine components that overlapped with the large-scale networks defined by Uddin et al. (2019), group differences in functional connectivity were found in four. All differences except one were located in middle and superior temporal regions. These temporal regions further showed connectivity differences between groups, dispersed across brain regions in frontal, parietal, and temporal regions as well as the cerebellum. The results suggest that deafness induces large-scale brain network reorganization which may be associated with behavioral adaptation due to the lack of access to auditory input in deaf individuals.

4.1. Large-scale brain networks

We show here that several large-scale brain networks are similar

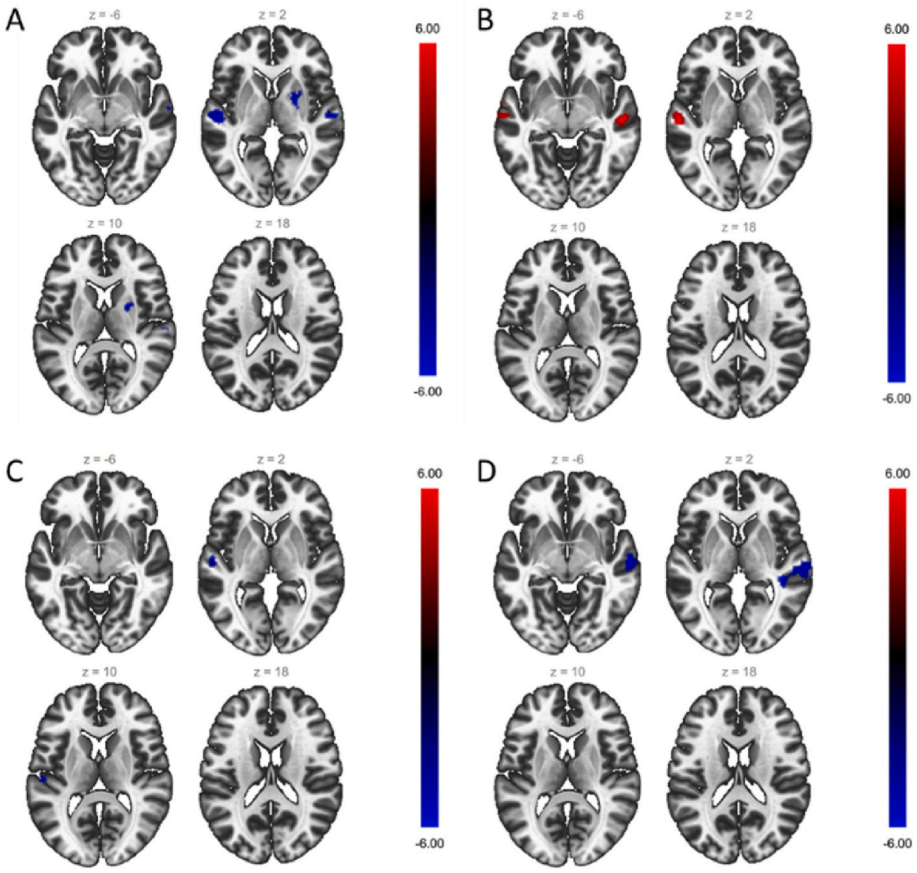


Fig. 2. Group difference in A) left control network (left lateral frontoparietal network), B) default network (medial frontoparietal network), C) ventral somatomotor network (ventral pericentral network), and D) attention network (dorsal frontoparietal network). Red represents clusters more strongly associated to the component for deaf early signers compared to hearing non-signers and Blue represent clusters more strongly associated to the component for hearing non-signers compared to deaf early signers.

Table 2
Peak coordinates for cluster with group differences.

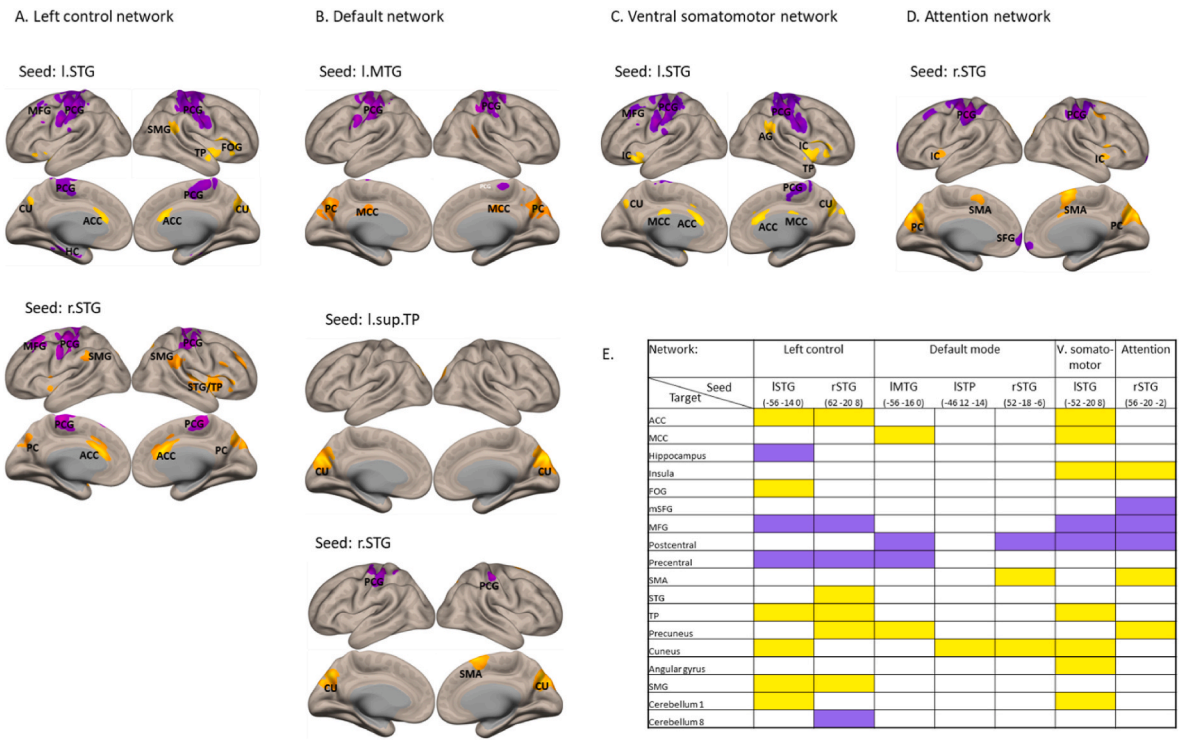
Network	Region of the peak[a]	Voxels	Peak MNI coordinates			DS > HN		HN > DS	
			x	y	z	*t*	p_{FDR}	*t*	p_{FDR}
Left control network	Left Superior Temporal Gyrus	189	−56	−14	0			4.55	<.001
	Right Pallidum	164	22	−2	6			5.52	<.001
	Right Superior Temporal Gyrus	124	62	−20	8			4.87	<.001
Default network	Left Middle Temporal Gyrus	189	−56	−16	0	5.63	<.001		
	Left Superior Temporal Pole	146	−46	12	−14	5.38	<.001		
	Right Superior Temporal Gyrus	144	52	−18	−6	6.05	<.001		
Ventral somatomotor network	Left Superior Temporal Gyrus	150	−52	−20	8			4.63	<.001
Attention network	Right Superior Temporal Gyrus	544	56	−20	−2			5.61	<.001

[a] Labels using AAL.

across deaf and hearing individuals. However, network organization of the left control, the default, the ventral somatomotor, and the attention networks seems to differ between groups. Specifically, middle and superior temporal regions are differently involved in these networks. Thus, using pre-defined network nodes based on hearing populations to compare network connectivity differences across deaf and hearing individuals might bias results, and confound interpretations.

Previous studies have found differences in engagement of the control network and the somatomotor network between deaf and hearing individuals and suggested this to be related to sign language and visual processing (Bonna et al., 2020; Cardin et al., 2018; Okada et al., 2016). We also found differences in connectivity within the attention network. Since this network is important for orientation towards external stimuli, including visual orientation and target detection, it is reasonable to assume that it might be reorganized in sign language users. Further, others have reported stronger functional connectivity for deaf compared to hearing individuals related to the default network (Bonna et al., 2020; Dell Ducas et al., 2021; Malaia et al., 2014) and between the default and the visual network (Bonna et al., 2020). While Bonna et al. (2020) suggested that the differences were associated with increased network integration following sensory deficits, Malaia et al. (2014) suggested a link to visual language processing since nodes within the default mode network are responsive to the processing of visual language.

Another explanation for observed differences between deaf and hearing individuals might be the influence of scanner noise, which in hearing individuals has been shown to contribute to suppression of the default network (e.g., Gaab et al., 2008). It should be noted that during scanning, hearing, but not deaf, individuals have auditory input, and this might influence how large-scale brain networks are captured in the signal. Except for effects on the default mode network (Gaab et al., 2008), scanner noise has also been shown to decrease activation in somatomotor networks (Andoh et al., 2017). Thus, the group differences we found in the somatomotor network might be even larger than what we would have found if scanner noise had been absent for the hearing



E.

Network:	Left control		Default mode			V. somato-motor	Attention
Seed / Target	lSTG (-56 -14 0)	rSTG (62 -20 8)	lMTG (-56 -16 0)	lSTP (-46 12 -14)	rSTG (52 -18 -6)	lSTG (-52 -20 8)	rSTG (56 -20 -2)
ACC							
MCC							
Hippocampus							
Insula							
FOG							
msFG							
MFG							
Postcentral							
Precentral							
SMA							
STG							
TP							
Precuneus							
Cuneus							
Angular gyrus							
SMG							
Cerebellum 1							
Cerebellum 8							

Fig. 3. Regions with stronger connectivity to the seeds from A) the left control network, B) the default network, C) the ventral somatomotor network and D) the attention network for deaf signers, compared to hearing non-signers, in yellow, and in purple for hearing non-signers compared to deaf signers. E) shows an overview of connectivity patterns between seeds and targets. ACC Anterior cingulate cortex; AG Angular gyrus; CU Cuneus; FOG Frontal orbital gyrus; HC Hippocampus; IC Insular cortex; MCC Middle cingulate cortex; MFG Middle frontal gyrus; PCG Pre-/postcentral gyrus; PC Precuneus; SFG Superior frontal gyrus; SMA Supplementary motor area; SMG Supramarginal gyrus; TP Temporal pole.

group. For the two remaining networks where there were differences between groups in the present study, that is, the control network and the attention network, Andoh et al. (2017) did not see that scanner noise influences connectivity. Nevertheless, the hearing brain is always exposed to sounds, whereas the deaf brain is not, and this is an inherent design features in studies such as the present one, i.e., we want to investigate potential effects of the lack of auditory input. To keep scanner noise as low as possible, all participants were given ear protection that, for the hearing individuals, reduced the sound to a level corresponding to speech or traffic noise. Thus, we believe that our findings represent meaningful between-group differences in brain organization, molded at least in part by differences in sound perception between groups. However, to further investigate the specific effects of scanner noise in comparisons between deaf and hearing individuals, sparse imaging procedures could be used.

We are not able to differentiate between the role of sign language and sensory deprivation with the current design, but the results of the present study, in combination with findings in previous studies, indicate that for individuals who do not process auditory stimuli, the inter-regional associations between auditory cortex and the control, somatomotor, and attention networks are functionally reorganized. This reorganization might in turn be associated with superior perceptual and/or cognitive functions related to visual processing.

In sum, the result from the ICA indicates that while several networks are similar across deaf and hearing individuals, some networks differ. Because existing network parcellations are based on hearing individuals, it is important to take our findings into consideration when using network nodes for investigating functional connectivity in deaf signers. For example, our results suggest that the salience network does not differ between groups, and pre-defined nodes should in that case be less problematic to use in group comparisons, whereas it might be more problematic to use pre-defined nodes for the default network, where we did see differences. Future studies should investigate and define large-scale brain networks in deaf individuals on larger samples to obtain a better basis for investigation of network nodes.

4.2. *Functional connectivity of the superior temporal cortex*

Although we did not see any group differences in the component identified as matching the salience network, the seeds placed in bilateral superior temporal gyrus showed stronger functional connectivity to the two main nodes within the salience networks, i.e., the anterior cingulate cortex and insula. This corroborates the finding from Ding et al. (2016) and is also consistent with results from congenital blind individuals. More specifically, Wang et al. (2014) identified stronger functional connectivity between the visual cortex and anterior insula (of the salience network) in congenital blind compared to sighted individuals. Thus, our results confirm previous findings of increased connectivity between sensory-deprived cortices and nodes of the salience network. In addition, here we show that this is not due to a difference across groups in the organization of the salience network, since we did not find such differences in the relevant ICA component. The driving factors for such reorganization might be the ability and the need for individuals with sensory deprivation to rely on, and identify, external stimuli with the remaining senses, requiring enhanced processing of such stimulus. Since the visual and the auditory cortices are typically not part of the salience network, these connectivity alterations may represent a functional shift (c.f., Cardin et al., 2020 and discussion below, in 4.3), such that sensory regions support the processing of salient stimuli and attention and aid effective switching between networks in the deaf group.

Several studies, including the seminal study by MacSweeney et al. (2006), have shown that the superior temporal cortex is important for language processing in the visual domain. While language input in the auditory domain enters the brain within the same lobe, language input from visual language must be conveyed there from the visual region, which might result in weaker functional connectivity within the superior

temporal regions for deaf compared to hearing individuals (Li et al., 2013). In the present study, we saw increased connectivity between the superior temporal cortex and supramarginal gyrus, precuneus, and cuneus in deaf signers, which may represent the link between input modality and processing of visuospatial components in sign language. Supramarginal gyrus is involved in the processing of sub-lexical components in both spoken and signed language (Malaia and Wilbur, 2010), but has been suggested to be specifically important for sign language processing (Corina et al., 1999; Emmorey et al., 2002). In deaf individuals, supramarginal gyrus is activated during the processing of sub-lexical structure of sign language (Corina et al., 1999; MacSweeney et al., 2008), i.e., hand configuration and hand placement, and preliminary data from our lab show an association between proficiency in sub-lexical processing of sign language and increased functional connectivity between supramarginal gyrus and superior temporal gyrus. Further, the supramarginal gyrus has been suggested to be involved in general coordination of hand movements, an ability required for successful sign language processing (Emmorey et al., 2002). Hence, increased connectivity between the supramarginal gyrus and the superior temporal cortex in deaf signers may represent the integration of spatial components in sign language processing. This interpretation is further supported by the finding that connectivity between the auditory cortex and supramarginal gyrus is stronger for deaf signers compared to hearing non-signers during a visual sign-based working memory task (Andin et al., 2021).

We found stronger connectivity for the deaf compared to the hearing group between the temporal seeds and the precuneus and cuneus. These regions are parts of the dorsal visual stream that process visual information related to spatial components of where a stimulus is and how it moves, also known as the "where"-stream. The dorsal visual stream has been suggested to be specifically susceptible to effects of deafness (Armstrong et al., 2002) and might contribute to superior processing of motion (Armstrong et al., 2002; Bavelier et al., 2001; Fine et al., 2005), faster detection of peripheral events (Bavelier et al., 2001; Dye et al., 2007; Proksch and Bavelier, 2002), as well as to inferior performance when visual distractors are introduced in the periphery (Holmer et al., 2020). In addition, Li et al. (2016) identified the cuneus as a network hub with increased functional connectivity to language processing regions in deaf, but not in hearing, individuals. A network hub is defined as a brain region of certain importance for communication between distributed brain networks (Hwang et al., 2013). Thus, the cuneus might play a different role in large-scale network organization for deaf and hearing individuals. In summary, increased connectivity with cuneus and precuneus may be important in reorganization following deafness, and the increased interaction with superior temporal regions may indicate an extension of the dorsal visual stream that carries visuospatial information about linguistic elements to the language processes carried out in the superior temporal cortex.

Language, be it spoken or signed, require motor skills; hands, arms, and the face for signed language, and throat, mouth, and face for spoken language. Therefore, different parts of the sensory-motor cortex and premotor regions are engaged during language production and processing, with the primary motor cortex activated during movements and the premotor regions engaged during the planning of movements (Finkl et al., 2020). In the present study, the largest cluster that showed different connectivity with the superior temporal cortex between groups was located in the sensory-motor cortex (pre- and postcentral gyrus), where hearing non-signers had stronger connectivity compared to deaf signers. This finding is in line with findings from both functional (Bonna et al., 2020) and structural (Finkl et al., 2020) connectivity. Finkl et al. (2020) investigated structural connectivity and found no differences between deaf signers and hearing non-signers within perisylvian language regions (including superior temporal cortex), but weaker connectivity between these regions and sensory-motor regions involved in speech. In a resting-state study, Bonna et al. (2020) found decreased functional connectivity between auditory and sensory-motor cortex in deaf signers. They suggested that this finding can be interpreted as a reduced need for fast feedback between auditory and speech motor areas for sign language users that do not use oral speech. We also found stronger connectivity for hearing compared to deaf individuals frontally to the sensory-motor cortex in the middle and superior frontal gyrus, regions that have been identified as sensitive to localization of sound in humans (for a review, see Plakke et al., 2014) and to audiovisual timing in non-human primates (Romanski and Hwang, 2012). Further, the deaf, compared to the hearing, group, showed stronger connectivity from right superior temporal gyrus to the supplementary motor region. This finding is consistent with functional resting state connectivity from Cardin et al. (2018). The supplementary motor area has further been found to be larger in deaf signers compared to hearing non-signers, which is suggested to be due to finger movements involved in fingerspelling (Kumar and Mishra, 2018). Hence, it is possible that enhanced connectivity between the superior temporal cortex and the supplementary motor area reflect modality-specific involvement related to features of sign language proficiency. The stronger connectivity for the deaf group between the superior temporal cortex and the supplementary motor area might thus represent similar functional processes as that between superior temporal cortex and sensory-motor cortex for hearing, although shifted frontally for deaf signers.

The hearing group further showed stronger connectivity between the seed in left superior temporal gyrus and hippocampus. We speculate that since the hippocampus is involved in memory formation and there is a tight connection between memory formation and sensory input, the connection between the auditory cortex and hippocampus is less important for deaf individuals. Tentatively, corresponding connections between the visual cortex and hippocampus would exist for deaf individuals. This could further be investigated by studying connectivity from hippocampus to auditory and visual cortex for deaf and blind as well as hearing, sighted individuals. Since hearing, sighted, individuals receive sensory input from both vision and audition, connections would appear from the hippocampus to both sensory cortices while deaf and blind individuals would show weaker connections to the cortices of the absent sense.

4.3. Reorganization based on functional preservation or higher-order cognition

Different explanations of how cross-modal reorganization is related to sensory deprivation are available (Cardin et al., 2018, 2020; Singh et al., 2018). Some emphasize purely neural processes unrelated to behavioral functions, while other focus on behaviorally driven associations. In the literature on deaf individuals, behavioral associations have been most thoroughly debated, and are represented in two theoretical lines (Cardin et al., 2020). The first proposes functional preservation, which assumes that brain regions without sensory input reorganize to respond to different sensory input, but with preserved function. For example, regions in the superior temporal cortex, that respond to speech in hearing individuals, respond to sign language in deaf signers, but not in hearing native signers (MacSweeney et al., 2002). The second theoretical line proposes a functional shift, such that brain regions of the absent sense reorganize to process higher-order cognitive tasks, for example working memory tasks (Twomey et al., 2017). There is empirical support for both theoretical claims, and it has been suggested that they can coexist (Cardin et al., 2020). The present study was not designed to specifically answer the question of whether auditory cortex reorganizes to functionally preserve or shift functions. However, we did find changed functional connectivity between the superior temporal cortex and several different brain networks. This might indicate a functional shift where the superior temporal cortex can support several other networks and functions in the absence of auditory input. If on the other side, the auditory cortex reorganizes to preserve functions in a new sensory modality, we would expect to find group differences in connectivity between sensory cortices, such as the visual cortex and

somatosensory cortex (which process tactile information). For example, when the auditory cortex is used as an extra resource for the processing of visual input, the connectivity between visual and auditory regions is likely to increase. However, we could not find any evidence for such reorganization. This is in contrast to previous task-based findings from both ourselves and others (Andin et al., 2021; Bola et al., 2017). We previously reported stronger connectivity for deaf compared to hearing individuals between the auditory cortex and visual cortices during a working memory task (Andin et al., 2021), and Bola et al. (2017) found similar results during a rhythm perception task. Hence, it is possible that auditory and visual regions are functionally connected by more efficient processing during task, but not during rest. Similar findings come from a study on blind individuals where an auditory task resulted in stronger occipito-temporal correlations compared to rest, while the opposite was found for sighted individuals (Pelland et al., 2017). Pelland et al. (2017) argue that these differences might stem from task-related cross-modal inhibition in sighted individuals together with occipital cortex involvement in auditory processing for blind individuals. Stronger connectivity during visual tasks in deaf individuals might reflect the same processes, indicating functional preservation in a task-based context. We found some evidence for increased connectivity in the deaf group between temporal and parietal regions, i.e., supramarginal gyrus, which could be a sign of visual language processing (Trettenbrein et al., 2021). However, we also found instances of stronger connectivity for hearing non-signers between temporal regions and the middle/superior frontal gyrus. Hence, although the results from the present study showed little evidence of functional preservation, there is evidence from other studies, primarily on task-based connectivity, that supports such an explanation. Weighing together the present results and earlier evidence leads to the conclusion that functional preservation and functional shift might co-exist (Cardin et al., 2020), but that the conditions during which observations take place (i.e., task-based or task-free data) will influence whether the former or the latter finds support in the data.

5. Conclusions

In the present study, we investigated large-scale brain networks in deaf signers and hearing non-signers using ICA. We identified nine components belonging to six large-scale networks. Four of the components showed differences between deaf and hearing individuals; the default, the left control, the ventral somatomotor, and the attention networks. The differences were primarily located to the temporal cortices. In the remaining network components, there were no differences between groups. Our findings suggest that, when using network nodes for investigating functional connectivity in deaf signers, it is important to acknowledge that the network parcellations available, which are based on hearing individuals, might not apply to deaf signing populations. Further, follow-up analyses on the group differences showed alterations in functional connectivity from the temporal cortex depending on group. Alterations might be related to the use of sign vs spoken language, visual attention differences, and differences in sensory input.

Credit author statement

Josefine Andin: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition. Emil Holmer: Conceptualization, Methodology, Software, Writing – review & editing.

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Declaration of competing interest

None.

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Appendix A. Supplementary data

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