TITLE: The organisation of working memory networks is shaped by early sensory experience

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ABSTRACT

We studied the reorganisation of linguistic and non-linguistic working memory (WM) processing as a consequence of sensory deprivation and sign language (SL) knowledge. We conducted an fMRI experiment in groups that differed in their hearing status and SL knowledge: deaf native signers, hearing native signers and hearing non-signers. Participants performed a 2-back WM task and a control task. Stimuli were signs from British Sign Language or moving nonsense objects in the form of point-light displays, allowing us to test, without low-level visual confounds, the extent to which WM for SL shares general visuo-spatial mechanisms.

We found characteristic WM activations in fronto-parietal regions in all groups. However, deaf participants also recruited bilateral posterior STC during the WM task, independently of the linguistic content of the stimuli, and showed less activation in fronto-parietal regions. Resting state connectivity analysis showed increased connectivity between frontal regions and STC in deaf compared to hearing individuals. WM for signs did not elicit differential activations, suggesting that WM for SL does not rely on modality-specific linguistic processing.

These findings suggest that WM networks are reorganised as a consequence of early deafness, and that the organisation of cognitive networks is shaped by the nature of the sensory inputs available during development.

INTRODUCTION

Early sensory loss results in crossmodal reorganisation of sensory cortices, where regions that usually process inputs from the missing modality are recruited by the remaining sensory modalities (Merabet & Pascual-Leone, 2010). Understanding this reorganisation is fundamental for gaining insights into the principles of neural plasticity and the functional capabilities of the human brain, including its potential for rehabilitation and enhancement.

Early deafness results in crossmodal reorganisation of regions which typically serve an auditory function, such as the superior temporal cortex (STC) (Finney et al. 2001; Karns et al. 2012; Cardin et al. 2013). It is likely that sensory loss will also impact the organisation of cognitive networks, given the strong interconnectivity between regions of the brain that support sensory and cognitive processing. However, it is not known to what extent reorganisation of STC has wider consequences for cognitive networks. The challenge in studying this issue in deaf humans is that cortical reorganisation is not only a consequence of lack of audition, but also of language being acquired in the visual modality, with acquisition is often delayed (Cardin et al. 2013). This late and insecure language development has consequences in adult language proficiency in signed and spoken language (Cormier et al. 2012), with corresponding effects in neural function (MacSweeney et al. 2008b; Mayberry et al. 2011; Pénicaud et al. 2013). Thus, differences in cortical reorganisation and cognitive performance between deaf and hearing individuals can be driven by the modality of language used by each group, by a delay in language acquisition, or by auditory deprivation (Lyness et al. 2013).

Visual WM represents an interesting case for the study of cognition and deafness, as it is one of the domains in which behavioural advantages have been observed for deaf individuals (Rudner et al. 2016; see Keehner and Atkinson, 2006, for a review). It is expected that this behavioural advantage will map into reorganised cortical pathways that support enhanced performance in the deaf. However, the neuroimaging evidence is inconsistent (Buchsbaum et al. 2005; Bavelier et al. 2008; Ding et al. 2015). In 2015, Ding et al. (2015) showed recruitment of STC during the delay period of a visual short term memory task in deaf individuals. This contradicted a previous study by Bavelier et al. (2008), which showed recruitment of typical fronto-parietal regions, but no activation of STC during maintenance. Buchsbaum et al. (2005) also showed STC recruitment for visual short term memory in the deaf, but constrained to a posterior region that is also recruited for spoken language and sign language WM in hearing signers, suggesting that this region is generally involved in linguistic WM, and not reorganised as a consequence of deafness.

Several factors may have contributed to the discrepancies, but language acquisition is likely to be an important one, given its relevance for cognitive development (Gathercole and Baddeley, 1993). Buchsbaum et al. (2005) and Bavelier et al. (2008) tested deaf native signers, a population in which sign language is acquired from birth, and where language development achieves the same landmarks in time as those of hearing children acquiring a spoken language. Instead, the group tested by Ding et al. (2015) was heterogeneous, with language acquisition likely to have been late and poor. It is unlikely that language proficiency will directly impact performance on a purely visuospatial task, such as the one used by Ding et al. (2015). However, given that language has been shown to mediate executive function in deaf children, including non-verbal WM (Marshall et al. 2015; Botting et al. 2016), it is likely that delayed and insecure language acquisition during childhood could have resulted in a different cortical reorganisation of cognitive networks during development (MacSweeney and Cardin, 2015). In a scenario in which superior temporal regions are not stimulated by auditory information, and in addition do not receive the necessary environmental language information to fully develop a role in language processing, it is possible that STC regions could end up taking on other cognitive functions such as working memory. In contrast, in the case of native signers, the environmental language input will be strong, and therefore the STC is potentially less likely to be recruited for working memory. Therefore, differences in language development and proficiency in the groups of deaf individuals tested in previous studies are likely to impact crossmodal reorganisation and the reorganisation of cognitive networks, potentially explaining the contradictory results of previous working memory studies.

Given the effect of language proficiency on cognitive development in deaf individuals (Marshall et al. 2015; Botting et al. 2016), it is important to determine whether deafness affects linguistic and non-linguistic WM differently. Previously, linguistic WM processing in deaf individuals has been studied using sign language stimuli (Buchsbaum et al. 2005; Bavelier et al. 2008). Results of these studies show that sign language WM in deaf individuals recruits parietal and occipital regions (Buchsbaum et al. 2005; Bavelier et al. 2008). Given that this pattern of results has also been found when studying sign language working memory in hearing signers, it has been suggested that this was an effect of more spatially oriented linguistic processing uniquely pertaining to sign languages (Rönnberg et al. 2004; Buchsbaum et al. 2005; Rudner et al. 2007; Bavelier et al. 2008; Pa et al. 2009). However, previous studies have focused on isolating linguistic processing by comparing sign language WM to spoken language WM. The rationale behind this design is that they are both linguistic WM, but relying on different sensory and motor processes: while sign languages are visual-manual languages, spoken languages are auditory-oral languages. However, neuroimaging studies have not compared sign language WM to purely visual WM. Therefore, it is not known whether differences in recruitment of parietal and occipital regions are related to modality-specific linguistic processing or to sensory processing. In other words, it is not clear whether these differences are due to more spatially orientated linguistic processing in sign language than in spoken language, or if they are driven by different sensory processing of the stimuli. Furthermore, none of those studies has shown additional recruitment of middle and anterior STC regions in deaf individuals.

Thus, several questions about the organisation of working memory networks in the context of auditory deprivation remain unanswered:

1. Does deafness result in recruitment of STC during working memory, suggesting reorganisation of cognitive networks as a consequence of auditory deprivation, or is this an effect of delayed language acquisition?
2. Is STC recruited for WM in deaf individuals only when the stimuli are purely visuo-spatial?

3. Are there linguistic WM mechanisms specific for sign language, and do they differ between deaf and hearing individuals?

The aim of this study is to address these questions by understanding whether the STC and cognitive networks involved in WM are reorganised as a consequence of early deafness, independently of delayed language acquisition. In addition, we aim to address whether differences in signed and spoken language WM are due to sensory or linguistic processing.

We conducted an fMRI experiment while participants performed linguistic and non-linguistic WM and control tasks. Our main group of interest were individuals who were congenitally deaf native signers of British Sign Language, and who thus have normal development of a first language. Hearing native signers and non-signers were also tested to determine whether effects were driven by auditory deprivation, or by sign language knowledge.

To segregate effects that are driven by general visuo-spatial processing of sign language stimuli from those that are driven by linguistic processing of signs, we used signs of British Sign Language and non-sense objects. A problem when comparing signs and other visuo-spatial stimuli, such as nonsense objects, is that there are differences between stimuli not only in linguistic content, but also in basic visual features, such as texture, colour, contrast and shape. To avoid these low-level confounds, we designed all our stimuli using point-light displays. Therefore, in all our experimental conditions, our stimuli had, on average, comparable low-level visual features.

We hypothesised that if deafness impacts the reorganisation of cognitive networks, differences in cortical recruitment for WM should be observed between deaf and hearing individuals. These differences should be independent of sign language knowledge, of the linguistic content of the information to be remembered, and be accompanied by a network-wise reorganisation for cognitive processing. Furthermore, if parietal and occipital areas are specifically recruited for sign language working memory as a consequenc of linguistic processing, we should observe stronger activations in these regions when deaf and hearing signers remember BSL stimuli.

METHODS

Participants

There were three groups of participants (Table 1):

A) Deaf signers (N = 12): congenitally severely-to-profoundly deaf individuals, who have at least one deaf parent, and are native signers of British Sign Language (BSL).

B) Hearing native signers (N = 16): hearing individuals who were born to at least one deaf parent who communicated with them from infancy using BSL.

C) Hearing Non-Signers (N = 16): hearing individuals who are native speakers of English and of another spoken language (native bilinguals), and who had no previous knowledge of BSL.

The decision to include native bilinguals of two spoken languages was made because native signers of BSL, both deaf and hearing, are also native or very proficient bilinguals, using spoken and written English as well as BSL. Deaf signers in Britain and in other countries, are usually bilingual to some extent, having different degrees of knowledge of the most used spoken language of the country where they reside. However, in the literature, they are often compared to groups of monolingual speakers. Here, we wanted to ensure that all three groups are bilingual in order to control for cognitive effects potentially related to using more than one language in everyday communication (Bialystok et al. 2012).

Participants were recruited from the UCL Psychology Subject Pool, the Subject Database of the UCL Institute of Cognitive Neuroscience, and the Participants Database of the UCL Deafness, Cognition and Language Research Centre. Participants were all right-handed (self-reported), had normal or corrected-to-normal vision and no history of neurological problems (self-reported). All participants gave their written informed consent to participate in the study, and were compensated for their time, travel and accommodation expenses. This study was approved by the UCL Ethics committee.

We recruited deaf and hearing native signers based on the criteria described above. Hearing non-signers were pre-screened, and participants were selected to match the other two groups on age and non-verbal intelligence, as assessed with the Block Design subtest of the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999); Table 1). To assess participants' WM skills, we also conducted a computerized version of the Corsi block-tapping task (Corsi, 1972) as implemented in PEBL software (http://pebl.sourceforge.net/), and an adapted computerized version of the operation span task (Turner and Engle, 1989), as reported in Andin et al. (2013). The maximum span length for the operation span was 5. To correct for ceiling effects and occasional inattention, the operation span was rated as the sum of the span of each correctly remembered sequence, times the proportion of times a sequence of such span was retrieved correctly. Two-sample t-tests were conducted to determine whether performance was significantly different between groups. Hearing signers had a significantly shorter span in the Corsi task than deaf signers ($t(26) = 3.4$; $p = .002$) and hearing non-signers ($t(30) = 2.2$; $p = .040$). Hearing non-signers scored higher than deaf signers in the operation span task ($t(26) = 2.1$; $p = .049$). None of the other between-groups comparisons of performance for Corsi and operation span tasks were significantly different ($p > .05$). Due to these significant differences, performance in the Corsi and operation span tasks were entered as covariates in all the behavioural and neuroimaging analyses. Gender was also entered as a factor in the analyses described below, because groups differed in numbers of males and females.

Stimuli

Our aim was to have stimuli that differed in terms of linguistic content, but were otherwise comparable. In particular, we wanted to minimise differences in visual features (e.g. colour, texture, contrast, illumination) that could drive responses in low-level visual areas, but also potentially engage different WM storage mechanisms due to their visual properties rather than their linguistic status. To this purpose, and based on theories of dynamic visual event perception (Runeson and Frykholm, 1983), all our stimuli were created as point-light displays. In this way, the unique components and global motion of the array were the same, but differences in the spatial location of the dots will result in the perception or not of biological motion of the hands.

Stimuli consisted of video clips of 21 signs of British Sign Language (BSL) and 21 nonsense 2-dimensional moving objects, presented as multi-coloured point-light displays (Johansson, 1973) on a black background (see Figure 1; Sup. Fig. 1). The BSL signs were created using a Qualysis Motion Capture System (Qualysis AB, Sweden), with markers on each of the joints of the right hand of the model. 3D coordinates from each joint were extracted, processed and displayed using Matlab 2010 (Mathworks, MA) and Cogent (www.vislab.ucl.ac.uk). Objects were created by matching the overall spatial location and global movement of the sign stimuli, but changing the arrangement of the dots from specific joints to nonsense shapes.

Signs were one-handed BSL lexical signs: ANGER, DANCE, DELICIOUS, DENMARK, DISAPPOINTED, DISLIKE, FEEL, KETTLE, LAUGH, LIKE, LIVE, PAINFUL, PETROL, PHONE, POOR, PREGNANT, RICE, SCHOOL, SHOCK, SMOKE AND WANT. One-handed signs were chosen in which the palm was parallel to the body, to avoid occlusion of the articulators which would make the point-light display difficult to capture and discriminate. Repetition of hand-shape across signs was matched with repetition of shape across objects. Average number of point-lights and duration of the display were also matched between signs and objects.

Each sign display contained three reference points: one corresponding to the nose of the model, and one corresponding to each of the shoulders. To avoid small jittering between the location of these points due to smalls movements of the model, the average position of the nose and shoulders was calculated from the sign stimuli and displayed in every video to provide static body references for the viewer. These reference points were also displayed for the object stimuli, to avoid gross differences in visual features between signs and objects. Participants were asked to fixate their gaze on the reference point corresponding to the nose, which was present throughout the experiment, including periods in which stimuli were not displayed. In future instances in this paper we will refer to the nose reference point as ‘fixation dot’.

To ensure that point-light signs were recognised as lexical BSL signs, and that nonsense objects were not misperceived as lexical signs, a larger set of 49 stimuli was included in a lexical decision pilot experiment. Four fluent BSL signers (three native, 1 early learner) took part in this test, and they were asked to decide whether each display was a real BSL sign or not. Following the behavioural pre-test, stimuli were revised to exclude ambiguous items. Only items that were correctly judged in at least 75% of the occasions were included in the final set of stimuli.

Tasks

Participants performed two types of task: a 2-back working memory task (Braver et al 1997) and a control colour task (Fig. 1; Sup. Fig. 1). In the 2-back WM task block, point-light displays were presented sequentially, and participants had to indicate whether the overall shape and movement of the display was identical to or different from the one seen two steps back. In the WM task, the colour of the dots was always varied to avoid participants performing the task by remembering the colour of specific dots. In the control colour task participants had to indicate if there were any yellow dots in the display. In short, for each display, they had to answer a ‘Yes’/’No’ question: ‘Is this display identical to the one 2-steps back?’ or ‘Are there any yellow dots in the display?’. Participants held a button box with both their hands. They were instructed to press one button with their thumb to indicate ‘YES’, and use the other thumb to indicate ‘NO’. Right and left thumbs were alternated for ‘YES’ and ‘NO’ responses across participants.

Before the experiment, the tasks were explained to participants in their preferred language (BSL or English), and written instructions were also provided in English. A short practice session ensured that participants were comfortable with all tasks. Point-light displays for the practice session were different from those used in the main experiment. The experimenters monitored participants’ performance during practice, answering questions and offering additional clarification as necessary in BSL or English.

Experimental Design

Our experiment had two types of stimuli and two types of task (2 x 2 design), resulting in four experimental conditions: WM Signs, WM Objects, Colour Signs, and Colour Objects. Each scanning session had 4 experimental runs; each run had 12 task blocks (3 of each condition), and each block had 12 trials. Blocks lasted ~28 s each, and they were separated by eight short fixation periods (2 - 3 s), and four long fixation periods (12 - 16 s). These were semi-randomly intercalated, avoiding occurrence of two long periods after consecutive blocks. Overall, each run lasted ~8.5min.

At the beginning of each block, a cue was presented for 1.5 - 2.2 s indicating the type of task participants would have to perform (either ‘memory’ or ‘colour’). This was followed by a green fixation dot for 1s, to indicate the task was going to start. After the presentation of the last stimulus of the block, the fixation dot changed colour to red for 1 s to indicate the end of the block.

Each block had either five 2-back matches, or four 2-back matches and 1 lure (ranging from 1-7 back steps). This arrangement was used for both the WM task and the colour task, but the identity of the display was not relevant for the colour task, and the colour task could not be performed by remembering the identity of the display. Of the 21 signs and 21 objects in the stimulus set, 7 unique items were chosen on each block of a particular condition. To specify the identity of the stimuli displayed, 48 block sequences were generated (4 runs x 12 blocks). To avoid any potential active or passive prediction, sequences were not repeated across conditions, and each participant was presented with each of the 48 sequences once. Sequences were randomly allocated to different conditions for each participant, meaning that all sequences had the same probability to be used for the WM task or the colour task. Additional sequences were created to specify the appearance of yellow dots in 4 – 5 trials of each block, achieving a similar 'ideal' distribution of 'yes' and 'no' answers across tasks. As explained above, colour could not be used to solve the WM task.

Image Acquisition

Images were acquired at the Birkbeck-UCL Centre for Neuroimaging (BUCNI) in London, UK, using a 1.5 T Siemens Avanto scanner and a 32-channel head coil.

There were two video cameras in the magnet's bore. One was used to monitor the participant's face and ensure they were relaxed and awake throughout scanning; the other monitored the participant's left hand which was used by deaf participants for manual communication with the researchers between scans. A third video camera in the control room was used to relay signed instructions to the participant via the screen. An intercom was used for communication with hearing participants. All volunteers were given ear-protection.

Stimuli were presented using MATLAB and Cogent. All stimuli were projected onto a screen hung in front of the magnet's bore; participants watched it through a mirror mounted on the headcoil.

There were five functional scans: 1 resting state and 4 task fMRI. Functional imaging data were acquired using a gradient-echo EPI sequence (36 slices, TR = 3060ms, TE = 50ms, FOV = 192 mm, 2 mm thickness, distance factor = 50%) giving a notional resolution of 3 x 3 x 3 mm. The first seven volumes of each run were discarded to allow for T1 equilibration effects. Each experimental scan lasted ~ 8.5 min (167 volumes). The resting state scan lasted ~ 10 min (196 volumes), and it was conducted at the beginning of the session. 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 acquired using magnetization-prepared rapid acquisition with gradient echo (MPRAGE, TR = 2730 ms, TE = 3.57 ms, 1mm^3 resolution, 176 slices).

Task fMRI Data Analysis

Task-fMRI data were analysed using MATLAB and Statistical Parametric Mapping software (SPM8; Wellcome Trust Centre for Neuroimaging, London, UK). Images were realigned, coregistered, normalised and smoothed (8 mm FWHM Gaussian kernel) following SPM8 standard pre-processing procedures. First-level analysis was conducted by fitting a general linear model (GLM) with 4 main regressor: WM signs, WM objects, Colour signs, and Colour objects. For each main regressor, RTs for each trial were modelled as a first-order parametric modulator. Other regressors included: right hand response, left hand response, cue period indicating a WM block, and cue indicating a colour block. For every regressor, events were modelled as a boxcar of the relevant duration, and convolved with SPM's canonical haemodynamic response function. Motion parameters were derived from the realignment of the images and included in the model as regressors of no interest. Regressors were entered into a multiple regression analysis to generate parameter estimates for each regressor at every voxel.

For each participant separately, contrasts for each individual condition were taken to a second level analysis, where the effects of deafness, task and stimulus type were tested as indicated in the results. Gender and performance in the Corsi and operation span tasks were included as covariates (analysis without Corsi and operation span as covariates revealed the same pattern of results for all contrasts). Effects and interactions of interest were tested using specified t-contrasts. Voxels are reported as x, y, z coordinates in accordance with standard brains from the Montreal Neurological Institute (MNI). Difference statistical thresholds are used for displays purposes, but activations are only discussed if they reached a significance threshold of $p < .05$ (FWE, corrected) at peak or cluster level.

Resting-state functional 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). Clusters that were differentially activated between hearing and deaf individuals during the working memory task were used as Regions of Interest (ROI) in the resting state connectivity analysis. The images were preprocessed following the same steps as in the task fMRI experiment. 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. 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 Y et al. 2007; Chai et al. 2012). Lastly, a low 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 (source) was then correlated with the signal of every other ROI (target), and normalised using Fisher’s r-to-z transforms.

RESULTS

Behavioural Results

During scanning, participants performed a WM task and a control colour task (see Methods). Reaction times and d’ for each condition are shown in Table 2. To evaluate whether participants performed the task at equal levels, a repeated measures ANOVA was conducted using reaction time as a dependent variable. Within-subject factors were Task (WM, Colour) and Stimulus Type (Signs, Objects); between-subject factors were Deafness (Yes, No), Sign Language Knowledge (Yes, No), and Gender (male, female). Performance in the Corsi and operation span tasks were entered as covariates. There were no significant main effects, but there was a significant interaction between Task and Deafness (F(1,36)

= 7.03, p = .012). Investigation of this interaction showed that deaf individuals were significantly faster for the WM task (Table 2; F(1,36) = 8.4, p = .006), but not for the Colour task (F(1,36) = 1.1 , p = .31).

A similar repeated measures ANOVA was conducted with d' as a dependent variable. There was a main effect of task (F(1,36) = 4.34, p = .045), where participants' performance was significantly better for the colour task (d' = 3.3 ± 0.11 s.e.m.) than the WM task (d' = 2.2 ± 0.12 s.e.m.). There was also a main effect of sign language knowledge (F(1,36) = 4.84, p = .034), with signers (deaf and hearing) (d' = 2.9 ± 0.12 s.e.m.) performing significantly better than non-signers (d' = 2.5 ± 0.16 s.e.m.) across all tasks and stimuli. No other main effect or interaction was significant (F < 2.8 and p > .1).

Given the significant interaction between deafness and task, RTs for each trial were included as modulators at the first level in the neuroimaging analysis. d' was not included in the main neuroimaging analysis because the statistically significant effects were not related to deafness. However, a model in which the d' for each run was included as a covariate in the second level analysis produced the same pattern of results.

fMRI Results

Stimulus Effects. A set of stimuli made of point-light displays was created for the purpose of this study. Behaviourally, we checked the validity of the stimuli in a pilot lexical decision task (see Methods). Validation of the stimuli was also the first step in the neuroimaging analysis, ensuring that the point-lights displays resulted in typical activations observed in the posterior temporal-occipital cortex for biological motion of hands (Pelphrey et al. 2005; Capek et al. 2008), and that they activated language-processing regions in signers (Neville et al. 1998; MacSweeney et al. 2002, 2008a; Emmorey et al. 2014). This was corroborated using the contrast [Signs > Objects] separately for each group (Fig. 2; Sup. Fig 2; Table 3). In the group of hearing non-signers, significant activations were observed in posterior temporal-occipital regions, regions activated by biological motion of hands as described above. Activations in this region were also found in both groups of signers; however, in these groups, activations associated with linguistic processing of the stimuli were also observed. Specifically, in hearing signers, there was additional recruitment of typical left-lateralised perisylvian regions for language processing. In deaf signers, instead, and presumably as a consequence of crossmodal plasticity, activations were more prominent along the STC. These results are in agreement with the literature on biological motion and the literature on sign language processing in hearing and deaf signers, confirming that our sign stimuli were perceived as moving body parts, from which linguistic information can be extracted.

Working memory effects. Neural activations elicited by WM were evaluated with the contrast [WM > Colour] across all groups of participants. This resulted in typical fronto-parietal activations for working memory (Fig. 3A; Table 4), including bilateral dorso-lateral prefrontal cortex (DLPFC), frontal eye fields, pre-supplementary motor area (pre-SMA), insula, intraparietal sulcus (IPS), precuneus, posterior middle temporal gyrus, and thalamus.

To understand the effects that congenital deafness has on cortical cognitive processing, we asked whether additional or different regions were recruited for WM processing in deaf individuals. To this effect, we first evaluated the group x task interaction [Deaf (WM > Colour) > Hearing (WM > Colour)]. This contrast showed activations along the whole length of the STC (Fig. 3B). To ensure that this finding was due to stronger activations for WM in the group of deaf individuals and not because of weaker activations in hearing individuals, we looked at the contrast [WM > Colour] for the deaf group, using the interaction contrast as a mask (Table 5). Figure 3B shows in red that the posterior regions of the STC, bilaterally, were recruited for WM in deaf individuals, but not in hearing participants (signers and non-signers). Parameter estimates further revealed that the differential activations in anterior portions of the STC obtained with the interaction contrast were due to deactivations during the WM task in hearing individuals, and not to recruitment of these regions for WM in deaf individuals (Fig. 3C). Deactivations in anterior STC were much reduced for WM in the group of deaf individuals, hence the significant result in the interaction.

To evaluate whether part or all of the WM effect found in posterior STC in the deaf group was a consequence of linguistic processing, we evaluated the interaction between task and stimuli with the contrast [(WM signs > WM colour) > (Colour Signs > Colour objects)]. This comparison also allowed us to identify mechanisms that were specific to sign language WM, and not general visual WM or task-independent linguistic processing. We tested this interaction separately for each group, and no significant activations ($p < .05$ FWE) were found. These results confirm that the effect of WM in the STC of deaf individuals is independent of the linguistic content of the stimuli. Therefore, as observed in the parameter plots in Fig. 3C, stronger activations were present for WM in both stimulus conditions: signs and objects. Furthermore, no specific activations for sign language WM were found either in signers or in non-signers.

The results presented above suggest that deaf individuals have the capacity to assign additional cortical resources to WM. It is possible that these extra resources reduce WM processing demands in fronto-parietal regions typically involved in this function. To evaluate whether any cortical regions were recruited to a lesser extent in deaf individuals than in hearing individuals during the WM task, we evaluated the interaction contrast [Hearing (WM > Colour) > Deaf (WM > Colour)]. For simplicity, from this point onwards, we will refer to this contrast as the reverse interaction. Results of the reverse interaction in Fig 4 and Table 6 show several fronto-parietal regions that were less active in deaf than in hearing individuals during the WM task (Fig. 4, blue clusters), including the left pre-SMA, DLPFC and inferior parietal lobule (IPL), and bilateral intraparietal sulcus (IPS). As can be seen in the top panel of Fig. 4 (blue clusters), the results obtained with the reverse interaction overlap with the fronto-parietal network recruited for WM in hearing individuals (Fig. 4, top panel, yellow clusters), suggesting that the additional recruitment of STC for WM in the deaf group is accompanied by non-recruitment - or weaker recruitment - of some fronto-parietal regions. To confirm this, we plotted the reverse interaction together with the contrast [WM > Colour] for the deaf group (Fig. 4, bottom panel, red clusters). The slices and parameter estimates in the bottom panel of Fig. 4 show that regions such as pre-SMA and the left IPL are indeed recruited for WM in deaf participants, but to a lesser strength than in the hearing group. Instead, parts of the left DLPFC and bilateral IPS are clearly recruited for WM in hearing participants, but not in deaf participants. These results support the idea that, during a WM task, the additional recruitment of STC in deaf individuals is accompanied by weaker recruitment of regions typically involved in this task in hearing individuals. This is in line with our previous study, in which we showed that the additional recruitment of STC for general visuo-spatial processing in deaf individuals is accompanied by weaker activity in occipito-parietal regions typically involved in these functions (Cardin et al. 2016). In the present study, we observed a similar trend in Fig. 2, where recruitment of STC for sign language processing in deaf individuals is also associated with weaker recruitment of left-lateralised perisylvian regions (Fig. 2; Sup. Fig. 2).

Functional Connectivity Analysis. Results from our task-based fMRI study suggest that, in deaf individuals, the STC is taking over some of the functions that in hearing individuals are performed by the fronto-parietal network for WM. If this is the case, the STC should somehow be incorporated into this functional network of fronto-parietal regions. Such incorporation can be measured in terms of functional connectivity during resting-state, when the low-frequency fluctuations of spontaneous activity of functionally related areas is highly correlated (Biswal et al. 1997). Therefore, if STC is part of the fronto-parietal network in deaf individuals, a correlation between activity in STC and in fronto-parietal regions should be found in the deaf participants, but not in the groups of hearing individuals.

To test this hypothesis, resting state functional connectivity was performed in a completely independent functional scan, which preceded the task-based fMRI and in which participants were not performing a task; therefore, connectivity results were not biased by our findings in the task-based fMRI. We hypothesised that if the STC is taking over some of the functions of fronto-parietal regions, a change in functional connectivity between the STC and the regions that are weakly recruited for WM should be observed as a consequence of deafness. Clusters significantly active for both interaction contrasts were used as ROIs in the connectivity analysis (Tables 5 and 6). These included: right and left STC, bilateral pre-SMA, left DLPFC, left IPL, and right and left IPS. For each group separately, the average signal from each ROI (source) was correlated with the signal of every other ROI (target). Figure 5 (Sup. Fig. 3) and Table 7 show the results of this analysis. In both groups of hearing individuals, signers and non-signers, significant positive correlations were found between frontal and parietal regions - this result is expected from ROIs which are part of the same functional network. Right and left STC were not positively correlated to any of these regions. In contrast, in the deaf group, STC is positively correlated to frontal regions. Specifically, in this group, activity in left STC is positively correlated to pre-SMA, and activity in right STC is correlated with activity in pre-SMA and left DLPFC. These correlations are not found in either hearing group. Two-sample t-tests were conducted to compare the strength of connectivity between STC and all other seeds in deaf and hearing individuals. Significant differences were found between deaf and hearing individuals in connectivity between pre-SMA and both right ($p = .03$) and left ($p = .01$)STC, and between right STC and left IPL ($p = .03$; Fig. 5; Sup. Fig. 3; Table 7). These results show a change in functional connectivity between STC and fronto-parietal regions, and suggest that the STC may be incorporated into a functional network for cognitive control in deaf individuals.

DISCUSSION

Early sensory experience shapes cortical organisation (e.g. Hensch, 2004). In cases of auditory deprivation in early life, crossmodal visual and somatosensory reorganisation has been found in cortices that usually have auditory functions (Hickok et al. 1997; Finney et al. 2001; Karns et al. 2012; Cardin et al. 2013). Here, we show that auditory deprivation also results in cortical reorganisation for cognitive processing. Three findings support this: recruitment of the STC for visual WM in deaf, but not in hearing individuals; weaker recruitment of fronto-parietal regions for WM in deaf than hearing individuals; and differences in functional connectivity between STC and fronto-parietal regions involved in WM as a consequence of auditory deprivation. Together, these results suggest a networkwide reorganisation for cognitive processing as a result of auditory deprivation itself, and not late and insecure language acquisition, nor the knowledge and use of a visuo-spatial language.

In addition, we found no evidence of linguistic WM mechanisms exclusive to sign language in either deaf or hearing signers, suggesting that sign language WM relies on general visuo-spatial and language networks.

Crossmodal Plasticity: Preservation of function vs Functional Shift

Crossmodally reorganised sensory cortices have been shown to preserve their original function but adapt to respond to a different sensory input (Lomber et al. 2010). This has been causally demonstrated by Lomber et al. (2010) in the auditory cortex of cats. Cooling specific cortical auditory areas, they showed that regions that in hearing cats are involved in processing sound localisation and sound movement, in deaf cats are respectively involved in visual localisation and visual motion. Importantly, this reorganisation conferred on deaf cats behavioural advantages over hearing animals. This preservation of function can also be observed in deaf humans, both for sensory and cognitive processes (Cardin et al. 2013). In that paper, it was shown that the left STC, which is usually involved in spoken language processing, is recruited for sign language processing, but not for general visuo-spatial processing.

In this study, we report a different type of plasticity as a consequence of auditory deprivation: the recruitment of STC for WM, suggesting a functional shift from the role this cortex has in hearing individuals. This kind of functional shift has also been observed in visual cortical areas of blind individuals, where responses to language have been found in regions which are usually involved in low-level visual processing (Röder et al. 2002; Amedi et al. 2004; Bedny et al. 2015; Lane et al. 2015). The differential recruitment between deaf and hearing individuals of STC and fronto-parietal networks for WM, accompanied by differences in resting state connectivity between these regions, suggests that the reorganised STC might be incorporated into a network for cognitive control. However, we cannot unequivocally assert this until the type of computation the STC is performing during WM is identified. It is possible that the STC is simply storing visual information, in the same way that, in hearing individuals, this region retains auditory information during working memory tasks (Linke and Cusack, 2015). The positive correlation between resting state activity in STC and frontal regions in deaf individuals, when participants do not have to do a working memory task, speaks against this argument, but to confidently reject this interpretation we need further evidence, from neuroimaging and electrophysiological studies, showing the type of information being represented in this cortex.

Another possibility is that the activity observed in STC during the WM task is an effect of language processing. As explained above, STC has been shown to be involved in language processing in deaf individuals (Neville et al. 1998; MacSweeney et al. 2002; Emmorey et al. 2011; Leonard et al. 2012; Cardin et al. 2013). Replicating this previous research, our results with the contrast [signs > objects] in the deaf group show bilateral activation of STC. Thus, the question arises whether this effect of WM is really a language effect. Although we cannot completely rule out this interpretation at this point, several pieces of evidence suggest that this is not the case: the WM effect is present with both signs and non-signs, so the recruitment of STC for working memory is independent of the explicit linguistic content of the stimuli. It could still be argued that participants verbalise their answers, and thus cause STC activations. However, it is not clear why only deaf participants would be using this strategy, as it would be expected that hearing participants would use a similar strategy, also recruiting STC. Furthermore, in their WM study, Ding et al. (2015) used a low-level visuo-spatial task in which participants had to remember the location of a grating. Here STC is also recruited for WM in deaf individuals, even though verbalisation is not likely to be a useful strategy given the large number of target locations.

STC is recruited for working memory in deaf individuals

Previous studies on deaf individuals were contradictory in relation to the recruitment of the STC for WM. Ding et al. (2015) showed recruitment of STC for visual short term memory in deaf individuals but not in hearing controls. However, it was not clear whether this effect was mediated by deafness *per se* or by secondary effects of language on cortical reorganisation (see below). Buchsbaum et al. (2005) also showed STC recruitment in their WM study, but constrained to left posterior regions. This result is similar to that obtained in a study of WM for speech and sign in hearing signers (Pa et al. 2009), suggesting that this region is generally involved in linguistic WM, and is not reorganised as a consequence of deafness. Furthermore, Bavelier et al. (2008) showed recruitment of STC in deaf individuals during visual short-term memory encoding, but not during the maintenance period, suggesting a sensory role for this cortex. Several differences between the experimental groups and tasks tested in these previous studies could explain the contradictory results. Buchsbaum et al. (2005) and Bavelier et al. (2008) tested deaf native signers, a population with normal language development. Instead, it is likely that on average the population of Ding et al. (2015) had late and insecure language development (spoken and signed), given early onset of deafness, and late onset of hearing aid use (average age 10.9 years) and late age of sign language exposure (average 6.8 years). This raises the possibility that some of the effects found by Ding et al. (2015) are not the result of deafness *per se*, but a secondary effect of late and insecure language acquisition. In this situation, the recruitment of STC for working memory, and perhaps other cognitive functions, could be a compensatory mechanism developed during infancy either because language cannot be used effectively to aid cognition or because the amount of language input is not enough to fully develop the function of STC in language processing. In either case, the recruitment of STC for WM will be the result of language delay, or language delay combined with auditory deprivation, but not an effect of sensory deprivation *per se*.

Thus, if the recruitment of STC for WM is driven by insecure or delayed language development, we will not see STC recruitment for WM in native sign language users, given that in this population language development is normal.

Alternatively, contradictory results in previous studies could be due to reorganisation of cortical networks in response to life-long experience with a sign language, which provides an additional source of variability when there is linguistic content in the tested stimuli. Buchsbaum et al. (2005) and Bavelier et al. (2008) used WM tasks with linguistic stimuli, whereas Ding et al. (2015) used basic visuo-spatial stimuli. Given that the STC is involved in sign language processing in deaf individuals (e.g. Cardin et al. 2013), it is possible that preserving this language function in native signers could have prevented its involvement in WM.

In this study, we specifically designed an experiment to address these contradictions:

1) We tested deaf native signers, who do not have language delay
2) We designed our stimuli to have linguistic and non-linguistic content, but used point-light displays, so that they could be directly compared without results being driven by differences in sensory features
3) We tested hearing non-signers and hearing native signers, as well as deaf native signers, to exclude the possibility that effects were driven by sign language knowledge, and not by deafness *per se*.

Using this design, we found that posterior portions of the STC are recruited for visual WM in deaf individuals. This STC recruitment is accompanied by weaker recruitment of fronto-parietal regions typically involved in WM, and by functional reorganisation of networks involved in cognitive processing. Our design allows us to assert that these effects are:

1) due to deafness *per se*, and not late and insecure language acquisition, as they were found in a deaf population who do not have language delay
2) independent of linguistic processing of the stimuli, as STC was recruited for WM when stimuli were signs from BSL and when they were nonsense objects.
3) independent of the native use of a visuo-spatial language, as these effects were found in deaf native signers, but not in hearing native signers.

Recruitment of the STC for WM in deaf individuals is largely constrained to its posterior portion, but the spatial extent of the recruitment we observed is bilateral and extends anteriorly beyond the left STC region reported by Buchsbaum et al. (2005).

Sign language WM vs spoken language WM

Signed and spoken languages differ in their underlying sensory and motor processes: while sign languages are visual-manual languages, spoken languages are auditory-oral languages. From a cognitive perspective, sign languages can be used as tools for investigating to what degree neural processes are based on, or are independent of, underlying sensory and motor mechanisms. Previous studies have shown great commonality in the cortical mechanisms supporting WM for signed and spoken languages (Rönnberg et al. 2004; Rudner et al. 2007, 2009; Pa et al. 2009), suggesting largely modality-independent mechanisms for linguistic WM. However, cortical activations elicited by signed and spoken language WM also differed in some important aspects. Specifically, there are activations for sign language WM in superior parietal and lateral occipito-temporal regions. Previously, it was not clear whether these differences were driven by sign-specific activations reflecting more spatially orientated linguistic processing in sign language than in speech, or if they were due to differences in the sensory properties of the stimuli.

By combining stimuli specifically designed to minimise differences in basic visual features, and groups of participants with and without knowledge of a sign language, in this study we were able to segregate effects that are driven by general visuo-spatial processing of the stimuli from those that are driven by linguistic processing. We found no effects that were specific to sign language WM. Therefore, we suggest that language modality differences between speech and sign WM found in previous studies of linguistic WM, are at least partially due to sensory differences in visuo-spatial and auditory processing, and not exclusive to linguistic WM mechanisms for sign language.

CONCLUSION

Here we have shown that deaf individuals recruit bilateral STC during WM, independently of the linguistic content of the stimuli. This is accompanied by a reduction in the recruitment of parietal and frontal regions typically associated with WM in hearing individuals, suggesting that the STC might be taking over cognitive functions usually performed by these fronto-parietal regions. Using resting state connectivity analysis, we also found a difference in the pattern of connectivity between frontal, parietal and STC regions between the deaf signers and hearing individuals, whether or not they were signers. This suggests a functional shift towards cognitive processing in STC as a consequence of crossmodal reorganisation.

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Table 1. Groups demographics and pre-screening tests.

	Age		Gender	WASI		Corsi		Operation Span	
	mean (range)	s.e.m		mean	s.e.m	mean	s.e.m	mean	s.e.m
Hearing Non-Signers (N =16)	28.3 (19-52)	2.1	7 m/9 f	60.1	1.1	5.7*	0.21	10.2**	0.28
Hearing Signers (N = 16)	29.9 (21-48)	2.1	5 m /11 f	57.6	1.9	5.2*	0.16	8.2	0.93
Deaf Signers (N = 12)	25.7 (19-33)	1.4	6 m/6 f	60.8	1.7	6.0*	0.22	8.4**	0.57
All Hearing (N = 32)	29.1 (19 – 52)	1.5	12 m/20 f	58.9	1.1	5.38	0.13	9.18	0.59
All Signers (N = 28)	28.1 (19 – 48)	1.4	11 m/17 f	59.0	1.3	5.54	0.16	8.29	0.59

Gender: m = male; f = female; * Significant differences between hearing signers and deaf signers (t(26) = 3.4; p = .002), and between hearing signers and hearing non-signers (t(30) = 2.2; p = .040). ** Significant differences between deaf signers and hearing non-signers (t(26) = 2.1; p = .049). s.e.m. = standard error mean.

Table 2. Performance in the working memory (WM) and colour tasks.

	d’								Reaction Times (ms)							
	Signs				Objects				Signs				Objects			
	WM		colour		WM		colour		WM		colour		WM		colour	
	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.	mean	s.e.m.
Hearing Non-Signers	1.81	0.19	3.15	0.17	1.95	0.19	3.23	0.17	1160	53.2	871	51.8	1149	57.0	870	52.2
Hearing Signers	2.30	0.16	3.58	0.19	2.39	0.19	3.70	0.19	1207	35.2	857	31.8	1177	39.8	821	31.3
Deaf Signers	2.36	0.68	3.10	0.89	2.46	0.71	3.15	0.90	1050	53.7	809	45.9	1052	56.6	792	46.2
All hearing	2.06	0.13	3.36	0.13	2.17	0.14	3.47	0.13	1186	31.6	864	29.9	1163	34.3	845	30.4
All signers	2.33	0.15	3.37	0.15	2.42	0.17	3.47	0.15	1140	33.4	837	26.6	1123	34.8	809	48.0

Table 3. Peak activations for the contrast [Signs > Objects]

Name		Peak Voxel				
		p (corr)	Z scores	x	y	x
Hearing Non-Signers						
Posterior temporal/Lateral occipital	R	< .001	5.5	48	-73	1
	L	.003	4.7	-45	-79	4
Hearing Signers						
Posterior temporal/Lateral occipital	R	< .0001	6.5	48	-70	1
	L	< .0001	5.8	-45	-67	7
Inferior Temporal Gyrus	L	.023	4.7	-42	-43	-14
Inferior Frontal Gyrus	L	.029*	3.6	-51	11	19
Deaf Signers						
Posterior temporal/Lateral occipital	R	.009	4.9	54	-70	1
Superior Temporal Cortex	L	.005*	4.0	-66	-37	7
	R	.019*	3.9	60	-13	-2

The table shows the activation peaks for the contrast [Signs > Objects] for each group separately. L: left. R: right. Corr: all values FWE corrected at p < .05, with the exception of *, which are FDR-corrected at cluster level.

Table 4. Peak activations for the contrast [WM > Colour] for all groups of participants.

		Peak Voxel			
Name		**Z scores**	**x**	**y**	**x**
DLPFC	R	> 8	45	29	28
	L	> 8	-48	11	28
Frontal Eye Fields	R	> 8	30	8	55
	L	> 8	-27	-1	58
Intraparietal Sulcus	L	> 8	-36	-46	43
	R	> 8	42	-43	49
Precuneus	L	> 8	-12	-64	52
	R	> 8	9	-64	52
pre-SMA	R,L	> 8	0	20	49
Insula	L	> 8	-30	23	-2
	R	> 8	33	23	-2
Posterior Middle Temporal Gyrus	L	> 8	-51	-64	-5
	R	7.1	57	-52	-5
Thalamus	R	6.1	9	-10	4
	L	5.8	-12	-16	10

The table shows the peak of activations for the contrast [WM > Colour] for all groups of participants. L: left. R: right. DLPFC: dorso-lateral prefrontal cortex. pre-SMA: pre-supplementary motor area. All peaks significant at p < .0001 (FWE corrected).

Table 5. Regions more active in deaf individuals for the working memory task.

Name		Peak voxel				
		p (corr)	Z score	x	y	z
Posterior Superior Temporal Cortex	L	< .001	5.94	-54	-43	16
	R	.004	5.30	48	-31	4

The table shows the peak of activations for the [WM > Colour] in the deaf group. Results were masked with an inclusive mask for the contrast [Deaf (WM > Colour) > Hearing (WM > Colour)], to include only voxels that were more active for the WM task only in deaf individuals (p<.005; inclusive masking). L: left. R: right. Corr: p value FWE corrected.

Table 6. Peaks of regions more active in hearing individuals for the working memory task.

		Peak Voxel				
Name		**p (corr)**	**Z scores**	**x**	**y**	**x**
pre-SMA	L	< .001	5.5	-3	17	55
Intraparietal Sulcus	L	.002	5.2	-21	-67	43
	R	.04*	4.0	30	-52	43
Inferior Parietal Lobule	L	.01	4.8	-48	-46	46
DLPFC	L	.026	4.65	-45	20	40

The table shows the peak of activations for the contrast [Hearing (WM > Colour) > Deaf (WM > Colour)]. L: left. R: right. Corr: all values FWE corrected at p < .05, with the exception of *, which is corrected at cluster level. DLPFC: dorso-lateral prefrontal cortex. SMA: supplementary motor area

Table 7. Resting-state functional connectivity results.

	Deaf Signers	Hearing Signers	Hearing Non-Signers
L STC – R STC	**0.637**	**0.631**	**0.609**
L STC – DLPFC	0.105	0.006	0.048
L STC – pre-SMA	**0.144***	0.008	-0.001
L STC – L IPL	-0.024	**-0.104**	**-0.121**
L STC – L IPS	-0.123	**-0.144**	**-0.095**
L STC – R IPS	**-0.192**	**-0.087**	**-0.110**
R STC – DLPFC	**0.116**	0.013	-0.004
R STC – pre-SMA	**0.163***	-0.004	0.030
R STC – L IPL	-0.001*	-0.060	**-0.208**
R STC – L IPS	-0.161	**-0.175**	**-0.165**
R STC – R IPS	**-0.163**	**-0.124**	**-0.138**
DLPFC – pre-SMA	**0.263**	**0.418**	**0.290**
DLPFC – L IPL	**0.328**	**0.569**	**0.380**
DLPFC – L IPS	**0.145**	**0.259**	**0.217**
DLPFC – R IPS	0.003	0.037	0.034
pre-SMA – L IPL	0.082	**0.197**	0.105
pre-SMA – L IPS	-0.030	0.100	-0.049
pre-SMA – R IPS	-0.117	-0.008	-0.086
L IPL – L IPS	**0.368**	**0.514**	**0.524**
L IPL – R IPS	**0.178**	**0.319**	**0.291**
L IPS – R IPS	**0.617**	**0.627**	**0.756**

The table show correlation coefficients of fMRI activity in resting state. Statistically significant coefficients are shown in bold (p < .05). * indicates connectivity of STC is significantly (p < .05) different between deaf and hearing individuals. L: left. R: right. DLFPC: Dorso-lateral prefrontal cortex. pre-SMA: pre-supplementary motor area. IPS: intraparietal sulcus. IPL: inferior parietal lobule. The right hemisphere is shown on the right. DS: Deaf Signers. HS: Hearing Signers. HNS: Hearing Non-Signers.

Figure Legends

Fig. 1. Experimental design and stimuli. A: Diagrammatic representation of a scanning run. ITI: inter-trial interval **B:** Structure of an experimental block. Using the same stimulus set, participants performed either a working memory (WM) task or a control colour task. In the experiment, point-lights were displayed in colour. For a colour version of the stimuli, please see Sup. Fig. 1. **C:** Representative examples of the stimuli. The dashed-arrow represents the pattern of movement of the display.

Fig. 2. Sign stimuli activate biological motion cortical areas in all groups, and language-processing regions in signers. The figure shows the results for the contrast [Signs > Objects] separately for each group of participants. Contrasts are displayed at $p < .005$, but only corrected results are discussed and reported in Table 3. A colour version of this figure can be found in Sup. Fig. 2.

Fig. 3. Superior temporal cortex (STC) is recruited for visual working memory (WM) in deaf individuals. A: Results of the contrasts [Working Memory > Colour] averaged across all groups and stimuli. The right hemisphere is shown on the right. Contrast displayed at $p < .05$, FWE. **B:** Results for the group x task interaction [Deaf (WM > Colour) > Hearing (WM > Colour)] are shown in green. Only posterior STC regions are more active for working memory in the deaf group (red clusters: overlap for the contrast [WM > Colour] in the deaf group and the group x task interaction). Both contrasts displayed at $p < .005$ for visualisation purposes, but all peaks significant at $p < .05$, FWE (see Table 5). **C:** Bar plots show parameter estimates from the peaks of the red clusters (top plots) and the green clusters (bottom plots). Bar represent means ± S.E.M.

Fig. 4. Weaker recruitment of fronto-parietal regions for working memory (WM) in deaf individuals. Top panel: The figure shows in blue the results of the group x task reverse interaction [Hearing (WM > Colour) > Deaf (WM > Colour)]. This interaction contrast is shown at $p < .005$ for display purposes, but results are discussed only if they achieved significance at corrected ($p < .05$, FWE) level (Table 6).

The contrast [Hearing (WM > Colour)] is shown in yellow (p < .05 FWE). **Bottom panel:** Results of the group x task reverse interaction are shown in blue, overlapped with results from the contrast [Deaf (WM > Colour)] in red (p < .001). The bar plots show parameter estimates (means ± S.E.M). L DLPFC, R IPS and L IPS: parameter estimates from peak voxels of the reverse interaction excluding those voxels that overlap with the contrast [Deaf (WM > Colour)]. Pre-SMA and L IPL: parameter estimates from peaks of the overlap between the reverse interaction and the [Deaf (WM > Colour)] contrast. L: left. R: right. DLFPC: Dorso-lateral prefrontal cortex. Pre-SMA: pre-supplementary motor area. IPS: intraparietal sulcus. IPL: inferior parietal lobule. The right hemisphere is shown on the right. DS: Deaf Signers. HS: Hearing Signers. HNS: Hearing Non-Signers.

Fig. 5. Differences in functional connectivity between STC and frontal areas in deaf and hearing individuals. The figure is a graphical representation of the resting-state functional connectivity results shown in Table 7. Significant resting-state correlation coefficients are indicated by a line joining two given ROIs. Black lines indicate positive correlations; grey lines indicate negative correlations. STC: Superior Temporal Cortex. DLFPC: Dorso-lateral prefrontal cortex. Pre-SMA: pre-supplementary motor area. IPS: intraparietal sulcus. IPL: inferior parietal lobule. Sup. Fig. 3 is a colour version of this figure.