

ORIGINAL ARTICLE

Working Memory for Signs with Poor Visual Resolution: fMRI Evidence of Reorganization of Auditory Cortex in Deaf Signers

Josefine Andin^{1,2}, Emil Holmer^{1,2,3}, Krister Schönström⁴ and Mary Rudner^{1,2,3}

¹Department of Behavioural Science and Learning, Linköping University, Linköping, Sweden, ²Swedish Institute for Disability Research, Linnaeus Centre HEAD, Sweden, ³Center for Medical Image Science and Visualization, Linköping, Sweden and ⁴Department of Linguistics, Stockholm University, Stockholm, Sweden

Address correspondence to Josefine Andin, Linköping university, IBL/I-huset, SE-581 83 Linköping, Sweden. Email: josefine.andin@liu.se.

Abstract

Stimulus degradation adds to working memory load during speech processing. We investigated whether this applies to sign processing and, if so, whether the mechanism implicates secondary auditory cortex. We conducted an fMRI experiment where 16 deaf early signers (DES) and 22 hearing non-signers performed a sign-based *n*-back task with three load levels and stimuli presented at high and low resolution. We found decreased behavioral performance with increasing load and decreasing visual resolution, but the neurobiological mechanisms involved differed between the two manipulations and did so for both groups. Importantly, while the load manipulation was, as predicted, accompanied by activation in the frontoparietal working memory network, the resolution manipulation resulted in temporal and occipital activation. Furthermore, we found evidence of cross-modal reorganization in the secondary auditory cortex: DES had stronger activation and stronger connectivity between this and several other regions. We conclude that load and stimulus resolution have different neural underpinnings in the visual-verbal domain, which has consequences for current working memory models, and that for DES the secondary auditory cortex is involved in the binding of representations when task demands are low.

Key words: deaf early signers, fMRI, *n*-back, sign language, visual resolution, working memory

Introduction

Working memory is the cognitive function that allows us to keep information in an accessible state for momentary processing (Baddeley and Hitch 1974; Ma et al. 2014), and the capacity of working memory is similar across the language modalities of sign and speech (Boutla et al. 2004; Andin et al. 2013). For both sign and spoken language, working memory processing elicits activation in a load-sensitive frontoparietal network (Buchsbaum et al. 2005; Rudner et al. 2007; Bavelier et al. 2008).

However, deaf signers, unlike hearing individuals, also recruit the auditory cortex during visual cognitive tasks, including working memory tasks (Bola et al. 2017; Cardin et al. 2018), and it has been suggested that the level of activation in this region increases with cognitive task demands (Twomey et al. 2017). Additionally, in working memory for speech, increased activity in frontal regions is not only observed for load manipulations but also when stimuli are degraded, suggesting that these manipulations rely on similar neurobiological mechanisms

(for a review see Peelle 2018). There is behavioral evidence suggesting that degradation of sign stimuli interacts with load in working memory for sign language (Rudner et al. 2015), but the neurobiological substrate of an overlap analogous to that found for speech has not yet been investigated. The purpose of the present study is to investigate the interaction of stimulus resolution and load in visual-verbal working memory for deaf early signers (DES).

Recent meta-analyses indicate that load manipulations in working memory *n*-back tasks reliably elicit neural activation in the left middle and inferior frontal gyrus, left anterior insula, right cerebellum, the anterior cingulate cortex, and left precentral gyrus (Mencarelli et al. 2019; Wang et al. 2019). According to resource models of working memory, capacity is determined by limited processing resources for dealing with the combined effects of the number of items to be recalled and the characteristics of the stimuli (Ma et al. 2014). This account is supported by not only brain imaging studies on working memory for speech that suggests overlapping activation in the frontal cortex for increased working memory load and increased degradation of stimuli (Smith and Jonides 1997; Peelle 2018), but also by the observation that working memory load and acoustic degradation results in similar changes in alpha oscillations (Obleser et al. 2012). Furthermore, in a study of auditory-verbal and visual-verbal (i.e. written language) working memory, Rodriguez-Jimenez et al. (2009) showed overlapping activation in frontal regions. In the context of language processing, the Ease of Language Understanding (ELU) model (Rönnberg et al. 2019) represents a working memory resource model that has been used to explain this overlap. According to the model, working memory resources are invoked by cognitive demands as well as a mismatch between an incoming linguistic stimulus and long-term memory representations. In the latter case, resources are used to repair the mismatch, so-called postdiction. In the present study, we tested the hypothesis that the common mechanism found in the auditory domain generalizes to the visual domain, which is expected based on a resource model of working memory (Ma et al. 2014; Rönnberg et al. 2019). Hence, if increased working memory load and decreased resolution are related to the same load-sensitive regions, we expect to find activation for low compared to high resolution in the regions identified as load-sensitive by for example Wang et al. (2019) and Mencarelli et al. (2019).

Sign language processing is dependent on brain networks similar to those which support speech processing, encompassing left-lateralized language regions (Rönnberg et al. 2000; MacSweeney et al. 2008). However, working memory for sign language generates stronger activation in auditory cortex and weaker activation in frontoparietal cortices for deaf compared to hearing individuals, which has been suggested to reflect deafness-related redistribution of cognitive functions from frontoparietal to temporal regions (Cardin et al. 2018). Both task-based (Bola et al. 2017) and resting-state connectivity patterns (Ding et al. 2016; Cardin et al. 2018) support the notion that reorganization of auditory cortex contributes to the involvement of this region in different types of visual tasks (Cardin et al. 2016; Ding et al. 2016; Bola et al. 2017; Cardin et al. 2018). Furthermore, Twomey et al. (2017) showed that different levels of sign language processing displayed distinct patterns of activation in auditory cortex in deaf, but not hearing, signers. In a picture-based similarity judgment task, they found more activation in left secondary auditory cortex during a phonological task than during a semantic or a visual task. In the right hemisphere homologue, however,

there was no difference in activation between tasks. Twomey et al. (2017) reasoned that the phonological task made greater demands on cognitive processing than the other two tasks and suggested that deafness alters the function of the left auditory cortex to support visuospatial cognitive processing, but that right auditory cortex merely supports low-level (i.e., sensory-perceptual) visual processing. However, previous studies have not directly investigated whether working memory load invokes activity in auditory cortex in DES, since load has not been manipulated. Here, we investigated this on activity in secondary auditory cortex.

Early evidence showed that adding Gaussian noise to videos of signs reduced their intelligibility for deaf signers (Pavel et al. 1987) and that presenting signs as point-light displays (Campbell et al. 2011) activated right frontal regions of the brain in addition to the network of regions typically supporting sign language processing. In a recent study, we showed that reducing the visual resolution of video-recorded sign stimuli reduced performance more when working memory load was higher (Rudner et al. 2015). In the present study, we used the same type of video materials as in Rudner et al. (2015) to investigate the neural correlates of reduced visual resolution in working memory.

To sum up, in the present study we investigated the effect of load and stimulus resolution on working memory networks and secondary auditory cortex in DES. To achieve this, we administered a sign-based *n*-back task to DES and hearing non-signers (HNS). We made three main predictions:

1. Reduced visual resolution of to-be-remembered signs will engage the load-sensitive frontoparietal working memory network, especially with increased load. We expected this to be reflected in behavioral performance, such that precision would decrease and response latency would increase with increased *n*-back load and decreased resolution. We also expected DES, who have access to previous representations of the presented signs, to be less affected by decreased resolution when *n*-back load was high. We further expected this to be revealed in fMRI data, such that reduced resolution and increased *n*-back load would show activation in load-sensitive regions as previously identified for *n*-back tasks; that is, middle and inferior frontal gyrus, anterior insula, cerebellum, and anterior cingulate cortex (Mencarelli et al. 2019; Wang et al. 2019).
2. Deaf compared to hearing participants will show less activation in the frontoparietal working memory network accompanied by more activation in superior parietal regions and in the temporal cortex (c.f. Cardin et al. 2018). Because the stimuli are meaningful for DES but not for HNS we expected to find that DES will show stronger activation in language-related regions while HNS will show stronger activation in regions related to visuospatial processing.
3. Cross-modal plasticity in secondary auditory cortex for DES will be indicated by a) stronger activation for DES compared to HNS, b) increased activation in the left hemisphere with increased *n*-back load for the deaf group, and c) stronger task-based connectivity to frontal and parietal regions in DES compared to HNS.

Method

Participants

Seventeen DES and twenty-four HNS were recruited to the study. Pregnancy, claustrophobia, and having non-MR compatible

Table 1 Group demographics and cognitive tests

	Deaf early signers		Hearing non-signers		t	p
	M	SD	M	SD		
Age	35.9	7.75	26.9	7.17	3.72	.001
Visual Puzzles*	11.2	3.60	12.4	2.39	1.20	.240
STS-SRT**	17.7	4.1				
	n		n		χ^2	p
Gender					0.43	.511
Female	9		10			
Male	7		12			
Education level					1.52	.469
Elementary	1		1			
High school	9		14			
University	6		7			

Note: *Standardized values (average performance = 10, with an SD of 3) from the measure of non-verbal cognitive ability.

**Swedish Sign Language Sentence Repetition Test.

implants were used as exclusion criteria. Inclusion criteria were right-handedness, normal or corrected-to-normal vision (Pelli and Robson 1988; McGraw et al. 1995), and normal or above normal non-verbal cognitive ability. Non-verbal cognitive ability was tested using the Visual Puzzles subtest from the Wechsler Adult Intelligence Scale (Fourth version, Wechsler 2008) and participants with scores below two standard deviations from the norm were excluded. Data from three participants (one deaf and two hearing) were excluded from the analyses due to cognitive screening or non-compliance during the fMRI experiment. Therefore, analyses are based on 16 DES and 22 HNS. All but one participant had completed at least high school (minimum of 12 years). Six deaf and seven hearing participants had university degrees. There were no significant group differences in gender distribution, non-verbal cognitive ability, or education level (Table 1). Due to recruitment constraints, the deaf group ($M=35.9$, $SD=7.75$) was significantly older than the hearing group ($M=26.9$, $SD=7.17$), $t(36)=3.72$, $P=0.001$.

All deaf participants used Swedish Sign Language (Svenskt teckenspråk; STS) as their primary language. Nine participants were deaf from birth and the remaining seven were between 6 months and 3 years when their deafness was discovered. Five participants had deaf parents who signed with them from birth. The remaining nine were exposed to sign language as soon as their deafness was discovered, and their parents could start sign language classes. Eight participants reported starting to use sign language before the age of three, while one participant reported learning sign language in pre-school years. Data on age of acquisition was missing for the remaining two participants. Deaf participants were tested using the STS Sentence Repetition Test (STS-SRT; Schönström 2014) and performed on par with an independent sample of deaf native signers from a previous study (Schönström 2014). Hearing participants were native Swedish speakers without any knowledge of STS.

All participants gave written informed consent and were compensated for travel expenses. The study was approved by the regional ethical review board in Linköping (Dnr 2016/344 – 31) and adheres to the ethical standards of the Declaration of Helsinki and to the EU General Data Protection Regulation.

Stimuli

The stimulus material consisted of video-recordings of signs lexicalized in STS that were produced by a male deaf native STS user. The videos were recorded with blue background at high

resolution. To control for material effects, two equivalent sets of materials were used (set A and set B). Each set consisted of 12 filmed signs. The sets were matched for semantic category (animals, food, and other) and grammatical content (i.e., sign composition regarding handshape, movement, and location). During the task (described below) videos were presented either in high or in low visual resolution (see examples in Figure 1). Low resolution was created by removing all high-frequency information from the videos. As a result, for signs in the videos with low resolution, handshapes were not distinguishable, making it difficult to correctly identify the sign. However, because the same signs were used for both the high and low resolution conditions, the training effect made it possible to guess the signs of low resolution with high precision, making the task linguistic for DES in both conditions. Stimuli were presented in the center of the screen with a resolution of 720×576 pixels and 25 frames per second regardless of the resolution of the individual stimuli. The screen was presented at a resolution of 800×600 pixels through MR-goggles (VisuaStim Digital, Resonance Technology, Inc.). The field of view, in the goggles, was 30° along the horizontal axis and 24° along the vertical axis. The task was presented using presentation software DMDX version 5.1.4.2 (Forster and Forster 2003).

Experimental task

Participants performed an *n*-back task with three load levels: 1-back, 2-back, and 3-back (Figure 1). Lists consisting of 22 two second long videos, with 240-ms interstimulus intervals, were presented. The task was to determine for each video whether the sign matched the previous sign in the list (1-back condition), the sign two steps back (2-back condition), or the sign three steps back (3-back condition). The participants were instructed to respond to each item presented by pressing one button on a button box held in their right hand with their index finger for “yes,” and another button with their middle finger for “no”. No feedback was given during the experiment. The dependent measure from the behavioral performance in the scanner was *d'* and latency in ms.

Experimental design

The experiment was set up as a $2 \times 3 \times 2$ design with group as between-group factor (DES, HNS) and load (1-, 2-, 3-back) and resolution (high, low) as within-group factors. Each scanning

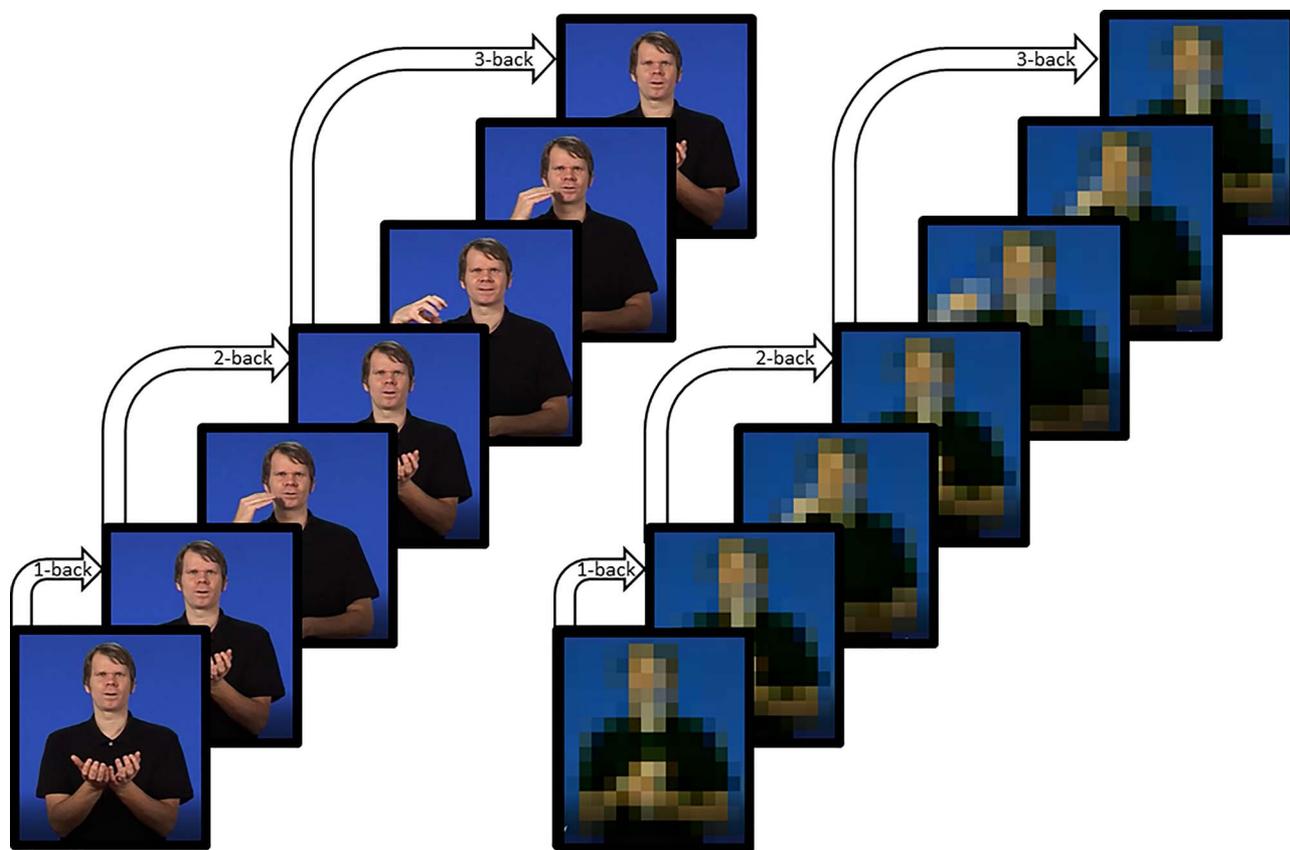


Figure 1. Schematic representation of the n -back task. Stimulus material from the present study; high resolution to the left and low resolution to the right. The English glosses of the signs presented here are from bottom to top: balloon, balloon, bear, balloon, octopus, bear, balloon.

session consisted of four experimental runs, each lasting 5 min and 43 s, and in which each load level was presented once at each resolution, that is, each run included six blocks. Blocks lasted for 49 s and were separated by 7 s fixation periods during which the letter “x” was visible at the center of the screen. Before the start of each block, a cue was shown for 2 s, indicating which task to perform (1-, 2-, or 3-back). No information about which resolution to expect was given. Each block had nine items that matched the item n steps back in the sequence and 13 items that did not match the item n steps back in the sequence. One of the non-matching items was a lure; that is, a sign that was repeated within the block but did not meet the n -back criterion. The purpose of the lures was to discourage response strategies.

For each set (set A and set B), eight lists of 22 items were created for each n -back load. The response pattern of the lists was the same in both sets. The lists were pseudorandomized into four standard runs that included two lists of each load level. The two lists from the same load level were always presented one after the other. For half of the participants, the first of the two lists at a given load level was in high resolution and the second was in low resolution, and for the other half of the participants the first was in low and the second was in high resolution. The runs were randomized into an individual run order for each participant. The same run order was used once in the deaf group and once in the hearing group.

Image Acquisition

MR imaging was performed on a 3 T scanner (Siemens Magnetom Prisma, Siemens Healthcare, GmbH) with a 64-channel

head coil at the Center for Medical Image Science and Visualization (Linköping University, Sweden). Functional images were acquired during continuous scanning using a BOLD multi-plex EPI sequence with the following specifics; FOV = 192×192 mm, voxel size $3 \times 3 \times 3$ mm, TR = 1340 ms, TE = 30, FA = 69° , number of slices = 48, 260 volumes per run, acquisition time 6 min per run, interleaved/simultaneous acquisition. Structural images were acquired in the beginning of the session using a T1 MPRAGE 3D-sequence; FOV = 288×288 , acquisition matrix = $208 \times 288 \times 288$, voxel size $0.90 \times 0.86 \times 0.86$ mm, TR = 2300 ms, TE = 2.36 ms, TI = 900 ms, FA = 8° . At the end of the experiment, a 10-minute-long resting brain EPI-sequence was acquired (data not reported here).

Statistical Analysis

Whole-Brain Analysis

Preprocessing and analyses of whole-brain fMRI-data were performed using Statistical Parametric Mapping packages (SPM12; Wellcome Trust Centre for Neuroimaging, London, UK) running under MatLab R2017a (The MathWorks Inc., Natick, MA). Preprocessing included realignment, co-registration, segmentation, functional and structural normalization, and spatial smoothing using a 10-mm FWHM Gaussian kernel, following standard SPM12 procedures. The realignment step showed that none of the participants moved more than 3 mm in x , y , z , or 3 degrees in pitch, yaw, and roll, and all data were retained for further analyses. Data from all four runs were analyzed for all participants, except in the case of one participant who performed only three experimental runs due to a technical problem.

First-level analysis was performed by fitting a general linear model with regressors representing the six different conditions (3 load levels \times 2 resolutions), as well as the six motion parameters from realignment. At the first level, individual regressors were entered into a 3×2 analysis of variance with load and resolution as within-subject factors. Contrast files pertaining to the main effects of load and resolution as well as the interaction effect between load and resolution were brought into second-level analyses. On the second level, tests of overall activation, main effect of group, resolution, and load as well as interactions between the factors were performed. Activations were considered significant if family-wise error (FWE) corrected P -values were < 0.05 at peak level.

Region of Interest Analysis

To investigate specific predictions concerning the secondary auditory cortex, region of interest (ROI) analyses were performed. Two ROIs were identified using the Anatomy Toolbox in SPM12; left and right secondary auditory cortex (consisting of TE3). From each ROI, a mean voxel value was obtained individually for each participant, and for each region, and analyzed in a $2 \times 3 \times 2 \times 2$ ANOVA, with group as between-group factor and load, resolution, and hemisphere as within-subject factors, using IBM SPSS statistics 24. Results were considered significant if $P < 0.05$.

Task-Based Connectivity

Task-based connectivity was performed using Conn—functional connectivity toolbox (version 17; www.nitric.org/projects/conn, RRID:SCR_009550). For each participant, ROI-to-ROI connectivity estimates were obtained by correlating the BOLD signal in seed regions (left and right secondary auditory cortex) with all ROIs and networks included in Conn. The realignment parameters were included as first-level covariates and group (DES, HNS) as second-level covariates. Denoising, including standard Conn procedures, was carried out to remove unwanted motion artifacts from the BOLD signal prior to calculation of connectivity measures. A band-pass filter of 0.008–0.09 Hz was applied. At the second level, differences in connectivity between deaf and hearing participants were analyzed across all conditions. Connectivity is considered significant if false discovery rate (FDR) $P < 0.05$.

Statistical Analyses of In-Scanner Data

In-scanner behavioral data were analyzed in two separate $2 \times 3 \times 2$ ANOVAs, one for latency (in ms) for correct responses, and one for the number of hits adjusted for false alarms using a d' measure, derived by subtracting a z -value for the number of false alarms from a z -value for the number of hits (Stanislaw and Todorov 1999). To correct for statistically infinite d' scores, 0.5 was subtracted from cases with maximum values of hits and 0.5 was added in cases with no false alarms. Analyses of behavioral data were performed using IBM SPSS statistics 24. For details of the design see “Experimental design”. The significance level for all tests was $P < 0.05$.

Procedure

Before arriving at the laboratory, participants filled in an online questionnaire with details of education, employment, and MR compatibility. The experimenter checked if the participants adhered to the inclusion criteria and scheduled them for testing. Upon arrival at the laboratory, participants were informed about

the study and signed the consent form. After this, testing began. Approximately, half of the participants started with behavioral testing and half with MR scanning. Behavioral testing included visual test, Visual Puzzles as well as a set of cognitive tasks not included in this study (e.g. Holmer et al. 2020). The behavioral testing lasted approximately 60 minutes in total. MR scanning, including the structural run, the experimental task, and a resting-state run, took approximately 45 min. Before scanning, the participants practiced the task outside the scanner, using materials not used in the experiment, until they could solve it reliably. A professional accredited STS interpreter was present at all times during the testing of deaf participants and provided verbatim translation of instructions. During scanning, instructions were repeated orally for hearing participants and in STS via a video camera for the deaf participants. Both deaf and hearing participants communicated with the experimenters between runs through a camera system or a sound system as appropriate.

Results

Behavioral Results

Latency (ms) and precision (d') from each n -back condition performed during scanning are presented in [Supplementary Table S1](#).

Response latency

For latency there were significant main effects of load, $F(2,72) = 114.4$, $P < 0.001$, $\eta_p^2 = 0.87$, resolution, $F(1,36) = 134.4$, $P < 0.001$, $\eta_p^2 = 0.79$, and group, $F(1,36) = 4.11$, $P = 0.05$, $\eta_p^2 = 0.10$. Latency was shorter for lower loads and high resolution, and DES responded faster than HNS. There was also a significant interaction effect between resolution and group, $F(1,36) = 11.2$, $P = 0.002$, $\eta_p^2 = 0.24$ (Figure 2a). Simple main effect analyses of the interaction showed that DES responded faster than HNS when resolution was high, $F(1,36) = 6.45$, $P = 0.016$, $\eta_p^2 = 0.15$, but not when resolution was low, $F(1,36) = 2.04$, $P = 0.162$, $\eta_p^2 = 0.05$. Both groups were faster at high than low resolution; DES, $F(1,36) = 96.3$, $P < 0.001$, $\eta_p^2 = 0.73$, and HNS, $F(1,36) = 40.4$, $P < 0.001$, $\eta_p^2 = 0.53$. Thus, contrary to our prediction the difference between DES and HNS decreased for low compared to high resolution. There was also a significant interaction effect between load and resolution, $F(2,72) = 13.5$, $P < 0.001$, $\eta_p^2 = 0.27$ (Figure 2b). Simple main effect analyses showed that latency was shorter for 1-back compared to 2-back ($P < 0.001$ for both high and low resolution) and 3-back ($P < 0.001$ for both high and low resolution), and shorter for 2-back compared to 3-back (high resolution $P = 0.011$, low resolution $P = 0.004$), and that latency was shorter for high compared to low resolution for all load levels (all P s < 0.001). The interaction between group and load was not significant, and the three-way interaction was not significant; hence, we found no support for our prediction of a larger difference between groups for low resolution when load increased.

Precision (d')

For d' there were also main effects for load, $F(2,72) = 172.4$, $P < 0.001$, $\eta_p^2 = 0.83$, and resolution, $F(1,36) = 76.5$, $P < 0.001$, $\eta_p^2 = 0.68$, such that precision was higher the lower the load, and the higher the resolution. However, in contrast to what we predicted no main effect of group was observed, $F(1,36) = 0.009$, $P = 0.927$, $\eta_p^2 = 0.0002$. There was a significant interaction effect between load

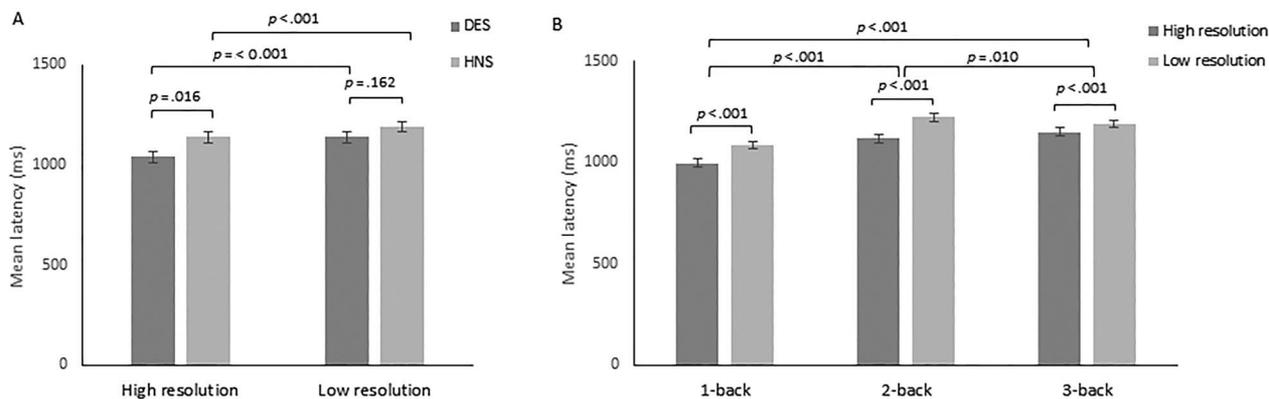


Figure 2. Interaction between a) group and resolution and b) load and resolution as measured by latency. Error bars represent SE.

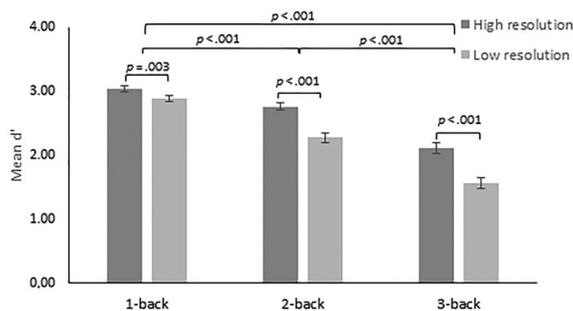


Figure 3. Interaction between load and resolution for precision as measured by d' . Error bar represents SE.

and resolution, $F(2,72) = 8.75$, $P < 0.001$, $\eta_p^2 = 0.20$ (Figure 3). Simple main effects of the interaction showed better performance for 1-back compared to 2-back and 3-back, and better for 2-back compared to 3-back (all $ps < 0.001$), and better performance for high compared to low resolution at 1-back ($P = 0.003$), 2-back ($P < 0.001$), and 3-back ($P < 0.001$). Unlike the results on latency, the interaction between group and resolution was not significant for d' , $F(1,36) = 0.014$, $P = 0.905$, $\eta_p^2 = 0.0004$. Again, we found no support for the prediction of a larger difference between groups for low resolution when the load increased; that is, there was no significant three-way interaction and no significant interaction between group and load.

fMRI Results

Whole-Brain Activation

Activation across all conditions showed a widespread pattern covering the frontoparietal working memory network as well as temporal and occipital cortices (Table S2 and Figure S1). To test our prediction that common regions are recruited for increased load and decreased resolution, whole-brain activation was evaluated by a $2 \times 3 \times 2$ ANOVA with group (DES, HNS) as between-subject factor, and load (1-back, 2-back, 3-back) and resolution (high, low) as within-subject factors. As expected, the main effect of load showed significant peak activation for 2-back and 3-back compared to 1-back in bilateral dorsofrontal regions within the frontoparietal working memory network (Figure 4 and Table 2). 1-back compared to 3-back load, also resulted in

activation within the frontoparietal network with significant peak activation in ventromedial frontal areas and in the middle temporal gyrus, and for 1-back compared to 2-back in the left superior frontal gyrus. These findings are in line with previously reported findings on the n -back paradigm (Mencarelli et al. 2019; Wang et al. 2019).

Contrary to our prediction, an effect of resolution was not observed in the frontoparietal working memory network. Instead, the main effect of resolution showed significant peak activation in occipital, parietal, and temporal cortices (Figure 4 and Table 2). High compared to low resolution revealed significant peak activation in bilateral inferior occipital and bilateral middle and superior temporal cortices, whereas low compared to high resolution showed significant peak activation in the right fusiform cortex and bilateral middle occipital cortex. Thus, although behavioral results indicated that both load and resolution manipulations influenced working memory load, imaging results revealed a decoupling of load and resolution effects, which suggests different mechanisms for working memory load and stimulus resolution in the visual-verbal domain.

Finally, in line with our prediction the main effect of group showed significant peak activation for deaf compared to hearing individuals in right superior temporal gyrus and in left middle temporal gyrus (Figure 4 and Table 2). However, contrary to our predictions, we found no evidence of stronger activation in frontoparietal regions for HNS and no significant activation for any interaction effect at the whole-brain level. The pattern of results remained the same when DES were analyzed separately (data not shown).

Region of Interest Analysis

To investigate the predicted reorganization of auditory cortex in DES we performed region of interest (ROI) analyses separately for right and left secondary auditory cortex. Results are shown in Supplementary Table S3 and depicted in Figure 5a and b.

As predicted, the analyses of variance showed a significant main effect of group, $F(1,36) = 18.4$, $P < 0.001$, $\eta_p^2 = 0.34$, such that the DES showed significantly stronger activation compared to HNS. We also predicted a specific effect of load in the left hemisphere for DES, which was not supported by our results. However, there was a significant interaction effect between group and hemisphere, $F(1,36) = 10.5$, $P = 0.003$, $\eta_p^2 = 0.23$. Simple main effects analyses showed stronger activation for deaf

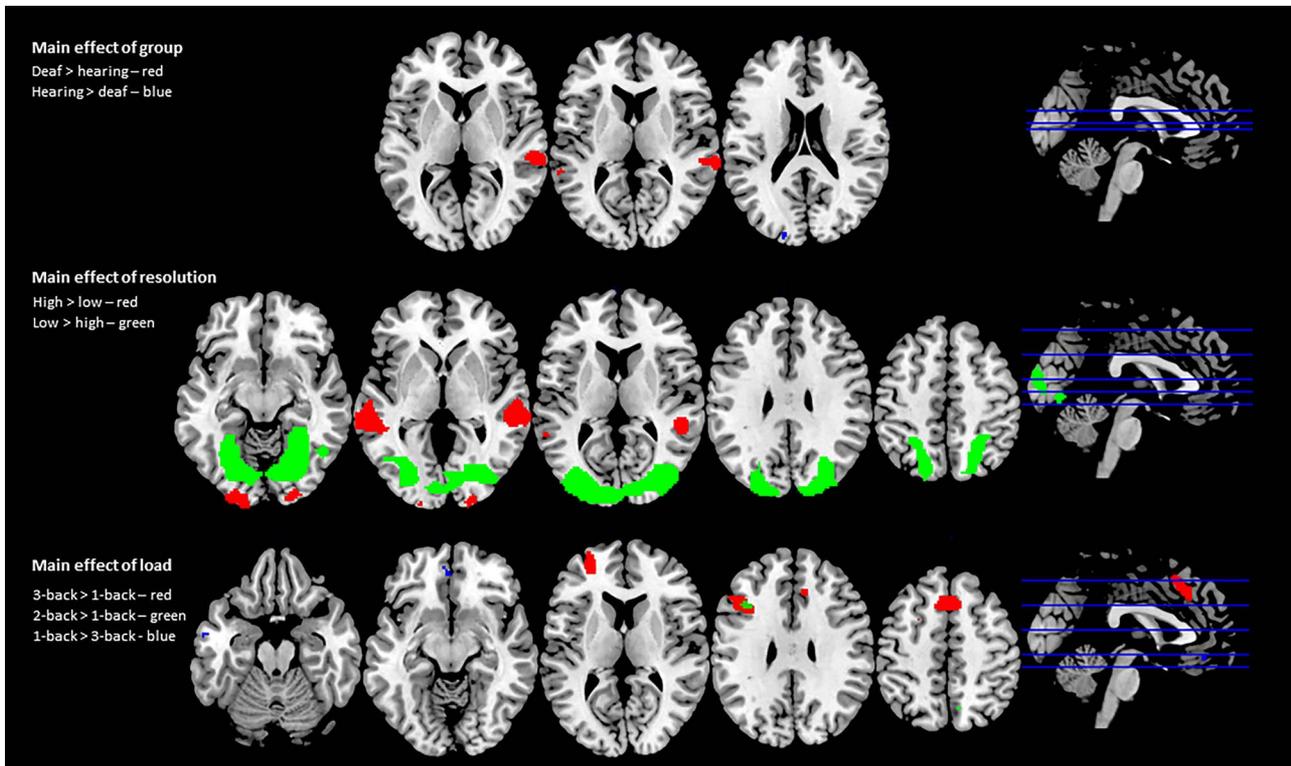


Figure 4. Significant activation for main effects of group (on top), resolution (middle) and load (bottom of the figure) superimposed on a normalized canonical image (ch2better template) using MRICron software. For the main effect of group, deaf > hearing is depicted in red and the opposite contrast in blue. For the main effect of resolution, high > low is depicted in red and the opposite contrast in green. For the main effect of load, 3-back > 1-back is depicted in red, 2-back > 1-back in green and 1-back > 3-back in blue. All contrasts are displayed at FWE-corrected $P < 0.05$ at peak level.

compared to hearing in both left, $F(1,36) = 9.23$, $P = 0.004$, $\eta_p^2 = 0.20$, and right hemisphere, $F(1,36) = 23.8$, $P < 0.001$, $\eta_p^2 = 0.40$, and significantly stronger deactivation in the right compared to the left hemisphere for HNS, $F(1,36) = 9.37$, $P = 0.004$, $\eta_p^2 = 0.21$, but not for DES, $F(1,36) = 2.74$, $P = 0.106$, $\eta_p^2 = 0.07$ (Figure 5C). Thus, the interaction was driven by HNS showing more deactivation in the right hemisphere. Interestingly, we also found a significant main effect of load, $F(2,72) = 6.69$, $P = 0.002$, $\eta_p^2 = 0.16$, and a main effect of resolution, $F(1,36) = 18.4$, $P < 0.001$, $\eta_p^2 = 0.34$, both indicating decreased activation as conditions become more challenging. All other effects were non-significant (see Table S3 for details).

Task-Based Connectivity

To further understand the role of secondary auditory cortex in cortical reorganization, task-based connectivity from this region was investigated. Especially, we tested the prediction that DES have stronger connectivity than HNS between secondary auditory cortex and pre-SMA, insula, anterior cingulate cortex, right IPL, and visual regions in the occipitotemporal lobes as previously shown (Ding et al. 2016; Bola et al. 2017; Cardin et al. 2018). Since there were no interaction effects between group and load or resolution in the ROI analyses, group differences in connectivity were investigated across all conditions. The ROI-to-ROI connectivity analysis showed that there was significantly stronger connectivity for DES compared to HNS between right secondary auditory cortex and bilateral lateral occipital cortex, bilateral fusiform cortex, left supramarginal gyrus, left inferior frontal gyrus as well as nodes in the visual lateral network and the salience network (Table S4 and Figure 6). Furthermore,

DES showed stronger connectivity, compared to HNS, between left secondary auditory cortex and bilateral occipital regions, precuneus, calcarine, and left supramarginal gyrus. There were no regions with stronger connectivity for HNS compared to DES. Thus, as for the results from the whole-brain and ROI analyses, connectivity results support the notion of a reorganization of the auditory cortices in cognitive processing for DES.

Discussion

The aim of this study was to investigate how working memory load and stimulus resolution affect activation of the frontoparietal working memory network and the auditory cortex in DES. We found that although behavioral performance decreased both with increasing n -back load and with decreasing visual resolution, the neurobiological mechanisms involved in diminished performance differed depending on the type of manipulation, and this applied both to DES and to HNS. These results contrast with previous reports concerning the auditory domain (Peelle 2018). Further, we found evidence of cross-modal reorganization of the secondary auditory cortex in DES.

Our first prediction was that poor visual resolution would increase working memory load and that this would be reflected in engagement of the frontoparietal working memory network. This prediction was supported by analysis of behavioral data, in terms of both reduced accuracy and longer latency. However, at the neural level, increased load and decreased resolution led to significant activation in different regions. As expected, we found stronger activation within the frontoparietal working memory

Table 2 Whole-brain peak activation for all significant main effects

Effect	Contrast	Peak voxel					Region
		p_{fwe}	Z-scores	x	y	z	
Group	DES > HNS	<0.001	5.68	69	-31	11	r. superior temporal gyrus
		0.001	5.35	57	-31	8	r. superior temporal gyrus
		0.005	5.04	-60	-40	11	l. middle temporal gyrus
	HNS > DES	0.020	4.69	-15	-91	20	l. middle occipital gyrus
Load	1-back > 2-back	0.011	4.77	-12	41	56	l. superior frontal gyrus (BA8)
		0.014	4.74	-6	56	-7	l. medial orbital gyrus (BA11)
	1-back > 3-back	0.029	4.56	-3	44	-10	l. medial orbital gyrus (BA11)
		0.014	4.74	-6	-49	23	l. post cingulum (BA31)
		0.030	4.56	-60	-4	-19	l. middle temporal gyrus (BA21)
	2-back > 1-back	0.004	5.01	-30	23	-1	l. insula (BA13)
		0.011	4.76	9	-64	50	r. precuneus (BA7)
		0.029	4.53	-39	20	29	l. inferior frontal gyrus (BA13)
		0.044	4.42	-27	50	11	l. middle frontal gyrus (BA10)
		3-back > 1-back	<0.001	5.82	-27	53	11
	<0.001		5.70	-9	26	41	l. superior medial gyrus (BA6)
	<0.001		5.61	9	29	32	r. middle cingulum (BA32)
	<0.001		5.57	3	26	44	l. superior medial gyrus (BA8)
	<0.001		5.70	-39	20	29	l. inferior frontal gyrus (BA6)
	<0.001		5.55	36	23	-4	r. insula lobe (BA47)
0.001	5.38		-30	23	-1	l. insula lobe (BA13)	
0.042	4.47		-27	8	53	l. middle frontal gyrus (BA6)	
0.043	4.46	27	8	56	r. superior frontal gyrus (BA6)		
Resolution	High > low	0.000	7.46	-21	-97	-13	l. inferior occipital gyrus
		<0.001	6.85	24	-97	-7	r. inferior occipital gyrus
		<0.001	5.91	54	-34	5	r. superior temporal gyrus
		0.001	5.43	57	-25	2	r. superior temporal gyrus
		0.001	5.43	-54	-40	5	l. middle temporal gyrus
	Low > high	0.001	5.40	-63	-34	2	l. middle temporal gyrus
		<0.001	Inf	24	-73	-10	r. fusiform
		<0.001	Inf	-21	-91	20	l. middle occipital gyrus
		<0.001	Inf	33	-85	20	r. middle occipital gyrus
		0.008	4.86	45	5	29	r. precentral

Note: The table shows activation peaks for each contrast, FWE-corrected at $P < 0.05$ at peak level. Brain regions are based on the cytoarchitectonic probability maps of the Anatomy Toolbox in SPM12. DES = Deaf early signers; HNS = Hearing non-signers.

network as load increased. In line with the recent meta-analysis on *n*-back tasks by Wang et al. (2019), this effect was observed exclusively in frontal and insular regions of the frontoparietal network. However, high compared to low resolution only showed activation in bilateral inferior occipital and bilateral temporal cortex, and low compared to high-resolution elicited activation only in the middle occipital and right fusiform gyrus. Taken together, these results suggest that manipulations of working memory load and visual resolution are governed by different neural mechanisms, which produce interacting behavioral effects. Obleser and co-workers investigated the effect of increased working memory load and stimulus degradation in the auditory domain in hearing individuals (Obleser et al. 2012) and individuals with hearing impairments (Petersen et al. 2015) and showed similar changes in alpha-oscillations for higher load and greater stimulus degradation. They concluded that both working memory load and acoustic degradation increase activation in a common alpha oscillatory neural network. Together with other evidence from the auditory domain this suggests a common neural mechanism for degradation and

load (Obleser et al. 2012; Alain et al. 2018; Peelle 2018; Rönnerberg et al. 2019), supporting resource models of working memory (Ma et al. 2014) and language processing (e.g., the ELU model, Rönnerberg et al. 2019). However, the lack of neural overlap in the present study challenges the validity of resource models of working memory in the visual-verbal domain, possibly reflecting modality-specificity within this domain (c.f. Rönnerberg et al. 2008; Holmer et al. 2016; Rudner 2018). Importantly, although the stimuli in our study were linguistically meaningful for DES but not for HNS, the pattern was the same across groups, indicating that the common mechanism suggested for auditory-verbal working memory does not generalize to visual-verbal working memory, regardless of language modality and hearing status. However, differing results across studies might also be related to the specific manipulations used. There is evidence from the auditory domain that brain activation differs between speech-in-noise, which requires suppression of competing auditory inputs, and segmented speech, which requires filling in the missing parts removed by spectral degradation (Davis and Johnsruide 2003; Alain et al. 2018). The cognitive demands seem

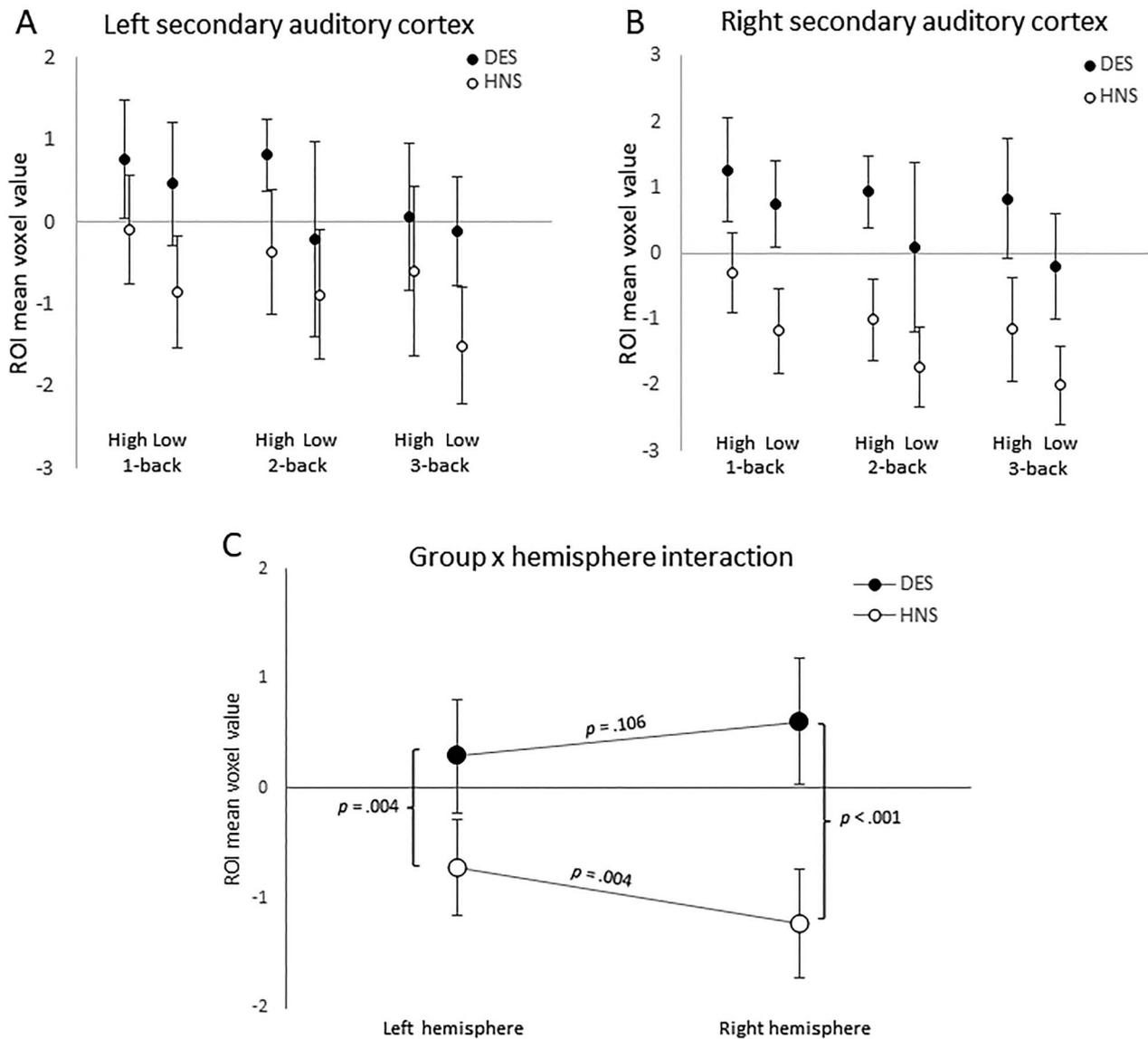


Figure 5. Activation within secondary auditory cortex ROIs. ROI mean voxel values from a) left auditory cortex and b) right auditory cortex are presented separately for each separate condition. The main effects of group, resolution, and load are significant. c) The significant interaction effect between group and hemisphere is shown. Error bars represent 95% CI.

lower for segmented speech manipulations, as reflected in no robust activation of frontal regions, accompanied by activation of primary sensory regions. The degradation manipulation in the present study is conceptually comparable to segmented speech, which might explain why we found no load-related activation. On the other hand, Obleser and colleagues (Obleser et al. 2012; Petersen et al. 2015) found overlapping activation for load and resolution using segmented speech. However, their finding of overlapping alpha enhancement was primarily in the temporoparietal regions and the cluster for memory load extended more into the frontal lobe compared to the cluster for resolution. In addition, the methodology they used measures another neural signature than fMRI, applied here, and is in addition poor in localizing the source of activation. Further studies should specifically investigate

the neural signature of type of stimuli manipulation across modalities.

Contrary to our prediction and to Cardin et al. (2018), we failed to find support for weaker frontoparietal activation in DES compared to HNS. On the other hand, following our prediction, DES had stronger activation in temporal regions compared to HNS. Thus, the present results lend only partial support to the notion that temporal regions take over cognitive functions typically associated with activity in the frontoparietal working memory network (c.f. Cardin et al. 2018). On the behavioral level, shorter latencies were observed for DES than for HNS, which may reflect more efficient visual-verbal processing skills associated with deafness (Bosworth et al. 2019). However, an interaction with resolution indicated that this processing advantage was only evident when resolution was high. For DES, this may reflect

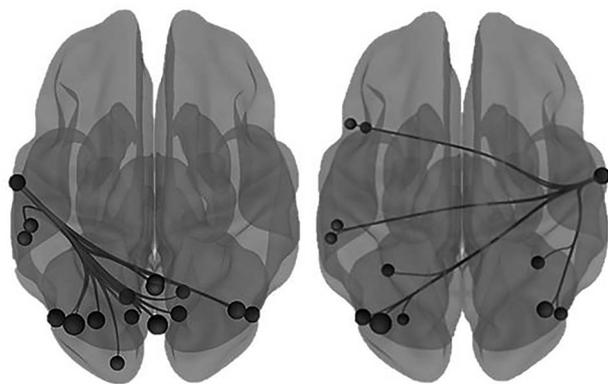


Figure 6. Overview of functional connectivity differences, between DES and HNS, from left secondary auditory cortex (left panel) and right auditory cortex (right panel). All marked connections were significantly stronger in the DES group, seed-level FDR-corrected $P < 0.05$.

fast lexical access when signs can be easily identified, leading to greater ease of language processing (Rönnberg et al. 2019). The processing advantage for DES revealed by shorter latency was not reflected in better accuracy. This suggests that lexical signs can be successfully stored in working memory irrespective of prior representation, even when processing speed differs. However, we did find group differences in neural activation in occipital and temporal regions, which may be related to use of different strategies. Our results showed that DES had stronger activation than HNS in bilateral temporal regions and stronger connectivity between temporal regions and both frontal and occipital regions. Contrary, HNS showed stronger activation than DES in visual cortices. These results might reflect a verbal strategy for the deaf group, for whom the task was linguistically meaningful, and a visual strategy for the hearing group, for whom the stimuli had no linguistic meaning. This notion is in line with results reported by Sanfratello et al. (2014), who showed activation towards temporal regions for individuals that used verbal strategies and activation mainly in the visual cortices for individuals that used visual strategies to solve a visual working memory task (c.f. Pearson and Keogh 2019). The same line of argument would also partly explain the activation related to resolution. High resolution provides a higher degree of verbal clarity than low resolution and may therefore be maintained in memory via verbal strategies, while low resolution has fewer verbal clues and requires a visual strategy, leading us to expect an interaction between group and resolution, which we did not find here. It is possible that low power in the present study obscured an interaction. An alternative explanation for the temporal activation found in DES is that it represents non-linguistic cross-modal reorganization, as shown in several previous studies (Cardin et al. 2013; Bola et al. 2017; Twomey et al. 2017; Cardin et al. 2018). In a recent study, Simon et al. (2020) found that observing biological motion results in stronger activation in superior temporal regions for deaf compared to hearing individuals, even when no linguistic information is conveyed. In summary, the temporal activation we found in the present study could be driven by cross-modal reorganization of visual processes and/or by different use of verbal strategies. To further investigate this, studies comparing different loads of both linguistic and non-linguistic biological motion are needed.

We predicted cross-modal reorganization to be represented by stronger neural activation in secondary auditory cortex in

DES compared to HNS and greater activation of left secondary auditory cortex in DES with increasing working memory load. As discussed above, we found stronger activation for the deaf compared to the hearing group in secondary auditory cortex bilaterally, which is partially in line with the results from Twomey et al. (2017) and Cardin et al. (2016, 2018). However, contrary to Twomey et al. (2017), we found, in the ROI analysis, that secondary auditory cortex was activated bilaterally, not only in the left hemisphere, and that with increasing task demands, activation decreased. Twomey et al. (2017) used three different tasks: phonological, semantic, and visual, with the phonological task showing the strongest activation. Thus, even though the tasks differed in difficulty, the study did not parametrically manipulate working memory load. This means that the results of Twomey et al. (2017) are not directly comparable with ours. While the hearing group showed deactivation in all but the simplest condition (where their activation did not differ from zero), the deaf group showed significant activation of secondary auditory cortex for 1-back and 2-back when the resolution was high and for 1-back when the resolution was low, and no significant activation or deactivation for higher loads. Hence, from the present findings, we suggest that the secondary auditory cortex is activated during sensory-perceptual processing of visual material for DES. From the present study design, it can, however, not be determined whether the group differences seen in auditory cortex depend on differences in hearing status or in language modality, or a combination of the two.

Finally, in line with our expectations, we found group differences in activation of secondary auditory cortex to be reflected in the task-based connectivity of this region. Specifically, we found stronger connectivity for DES compared to HNS between both the right and the left secondary auditory cortex and occipital as well as parietal regions. The finding of stronger connectivity between auditory cortex and occipital regions is in line with Bola et al. (2017) and might reflect coupling of regular visual processing in occipital regions with visual-verbal processing in auditory regions in sensory-perceptual integration, resulting from the cross-modal plasticity that arises from deafness and/or sign language use. In a resting-state study, Ding et al. (2016) found stronger connectivity between auditory cortex and bilateral insula for deaf signers and suggested that insula acts as a hub where relevant stimuli are identified and forwarded to executive networks that are involved in working memory, attention, and other higher order cognitive processes. Our results of stronger connectivity for DES compared to HNS between right secondary auditory cortex and the left insula provides further support for this notion. Unlike Ding et al. (2016) and Cardin et al. (2018), we found no evidence of stronger connectivity between secondary auditory cortex and pre-SMA, left intraparietal lobule, or cingulate cortex in DES compared to HNS. However, those studies used resting-state data and are therefore more likely to reflect the default mode network (Horn et al. 2014) rather than working memory processing. Finally, we also found stronger connectivity for DES compared to HNS between the right secondary auditory cortex and the left inferior frontal gyrus. This could reflect the linguistic nature of the task at hand for the DES (Hickok et al. 1996; MacSweeney et al. 2008), and is in line with findings from auditory-verbal working memory (for review see Buchsbaum and D'Esposito 2019). In sum, the connectivity and ROI results here provide further evidence of auditory cortex being a site of cross-modal plasticity in DES and that they, due to the reorganization, can take advantage of the processing capacity offered by this region in visual tasks.

It should be noted that the age difference between groups might be a confounding factor in the present study, for example, earlier work suggests that the pattern of neural activation for *n*-back tasks might change with increasing age (Yaple et al. 2019). However, such changes have been reported for other regions (e.g., prefrontal cortex, parietal lobe) than those for which we here find group differences. Thus, it is unlikely that the age difference between groups in the present study explains the group differences we see in neural activation.

Conclusion

We show here that the behavioral performance decrements caused by load and resolution have different neural underpinnings in the visual domain, and that these neural mechanisms do not differ between DES and HNS. The bilateral temporal regions activated for high-resolution stimulus were also engaged more by DES than HNS, indicating the use of a verbal strategy to solve the task. Stronger activation in occipitoparietal regions for low-resolution stimulus and for HNS compared to DES might indicate the use of visual strategies. Furthermore, the results of the current study add to earlier studies by showing cross-modal reorganization of the secondary auditory cortex. However, we found no support for increased involvement of this region in dealing with increasing cognitive demands. We suggest that for DES, the temporal cortex has a general role in sensory-perceptual processing of visual materials, in particular the binding of representations in tasks where cognitive demands are low.

Supplementary Material

Supplementary material can be found at *Cerebral Cortex* online.

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Notes

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