Increased functional connectivity between the auditory cortex and the frontoparietal network compensates for impaired visuomotor transformation after early auditory deprivation

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Abstract

Early auditory deprivation leads to a reorganization of large-scale brain networks involving and extending beyond the auditory system. It has been documented that visuomotor transformation is impaired after early deafness, associated with a hyper-crosstalk between the task-critical frontoparietal network (FPN) and the default-mode network (DMN). However, it remains unknown whether and how the reorganized large-scale brain networks involving the auditory cortex contribute to impaired visuomotor transformation after early deafness. Here, we asked deaf and early hard of hearing (DHH) participants and normal hearing (NH) controls to judge the spatial location of a visual target. Compared to NH controls, the STG showed significantly increased functional connectivity with the FPN and the DMN in DHH participants, specifically during egocentric judgments. However, increased STG-FPN and STG-DMN coupling showed antagonistic effects on egocentric judgments. In DHH participants, increased STG-FPN connectivity was associated with improved egocentric judgments, while increased STG-DMN connectivity was associated with deteriorated performance in the egocentric task. Therefore, the data suggest that the auditory cortex exhibits compensatory neuroplasticity (i.e., increased functional connectivity with the task-critical FPN) to mitigate impaired visuomotor transformation after early auditory deprivation.

Keywords: connectomics, deaf and early hard of hearing, modularity, neural plasticity, superior temporal gyrus

Introduction

The spatial orientation of an object can be represented in either egocentric (i.e., relative to the viewer's body/body effectors) or allocentric (i.e., relative to other external objects) reference frames (Paillard 1991; Blouin et al. 1993; Burgess 2006). The egocentric reference frames are particularly critical for guiding smooth visually-guided actions, which requires transforming visuospatial representations of external visual objects into visuomotor representations (Galati et al. 2001; Cohen and Andersen 2002). At the neural level, the dorsal attention network (DAN) is involved in coding the general visuospatial representations underlying both the egocentric and allocentric reference frames (Committeri et al. 2004; Chen et al. 2012, 2014; Gomez et al. 2014), while the frontoparietal network (FPN) is specifically involved in body-centered visuomotor transformation during the egocentric task (Galati et al. 2000; Committeri et al. 2004; Neggers et al. 2006; Chen et al. 2012, 2014). The deaf and early hard of hearing (DHH) people exhibited superior haptic orientation processing compared to both normal hearing (NH) signers and non-signers, i.e., with the effect of sign language controlled for (Van Dijk et al. 2013). Additionally, they made more orientation errors for the crossed posture condition during the crossed-arm temporal order judgment task (Sharp et al. 2018). These findings suggested that early auditory deprivation shifts the balance of reference frames. Since auditory signals interact with the tactile and the motor system during posture, balance, and movement initiation (Queralt et al. 2008; Kanegaonkar et al. 2012; Gandemer et al. 2017), early auditory deprivation might impair these body-related motor processes (Houde et al. 2016; Sharp et al. 2018). Accordingly, previous evidence from our lab shows that processes relying on the egocentric reference frame are impaired after early auditory deprivation (Zhang et al. 2014). The latter is associated with an abnormal hyper-crosstalk between the task-critical FPN and the task-negative default-mode network (DMN) during body-centered egocentric judgments in the DHH individuals (Li et al. 2022).

Early auditory deprivation leads to structural and functional reorganization of the auditory cortex (Amaral and Almeida 2015; Cardin et al. 2020; Hribar et al. 2020; Simon et al. 2020; Yusuf et al. 2021, 2022), which is mainly located in the superior temporal gyrus (STG) (Morosan et al. 2001, 2005). Structurally, decreased fractional anisotropy of white matter fibers, decreased white matter volume, and increased cortical thickness have been observed in the auditory cortex of DHH people compared to NH controls (Emmorey et al. 2003; Smith et al. 2011; Karns et al. 2016; Kumar and Mishra 2018). However, it remains unknown whether these brain structural changes in the DHH people, such as the increased cortical thickness of the auditory cortex, are associated with impaired visuomotor transformation. Functionally, early auditory deprivation causes cascading neurological and neurocognitive changes (Kronenberger et al. 2014; Kral et al. 2016). Especially, the auditory cortex of the DHH people undergoes cross-modal reorganization and starts to process stimuli from the remaining sensory modalities, such as visual and vibrotactile stimuli (Levänen et al. 1998; Karns et al. 2012; Ding et al. 2015; Bola et al. 2017; Cardin et al. 2018). Further, altered task-evoked or intrinsic functional connectivity between the auditory cortex and other brain regions have been revealed during a variety of cognitive tasks (Shiell et al. 2015; Ding et al. 2016; Benetti et al. 2017, 2021; Bola et al. 2017), indicating large-scale network reorganization in the DHH people. For example, besides the large-scale network reorganization beyond the auditory system (Li et al. 2022), the auditory cortex of the DHH people exhibits stronger intrinsic connections with sub-regions of the DMN and the FPN compared to NH controls (Ding et al. 2016; Cardin et al. 2018; Andin and Holmer 2022). However, it remains unclear how the decreased network segregation between the 'deprived' auditory system, the task-critical DAN and FPN, and the task-negative DMN contributes to the impaired visuomotor transformation after early auditory deprivation. To answer how the structural changes and the large-scale network reorganization involving the auditory cortex are associated with impaired visuomotor transformation in DHH individuals, we re-analyzed the data from a previous fMRI study (Li et al. 2022).

For the network analyses, we focused on the cross-modal reorganization of the functional connectivity between the STG, the task-critical DAN and FPN, and the task-negative DMN in the DHH individuals during an egocentric judgment task. If the task-specific reorganization of a large-scale brain network involving the STG helps compensate for the impaired visuomotor transformation after early auditory deprivation, we expected that: (1) compared to the NH controls, the STG should show enhanced between-module connectivity with the task-critical FPN in the DHH individuals, specifically during the egocentric task; and more importantly (2) the potentially enhanced STG-frontoparietal connectivity should be associated with improved egocentric performance in the DHH people. Moreover, we have previously revealed that impaired visuomotor transformation after early auditory deprivation is associated with abnormal hyper-connectivity between the task-critical frontoparietal regions and the DMN (Li et al. 2022). Therefore, if the STG in the DHH individuals' brain is reorganized to be more integrated, as manifested in increased functional connectivity with the frontoparietal regions during the egocentric task, it may also exhibit increased connectivity with the DMN. Moreover, similar to the increased FPN-DMN connectivity, the potentially increased STG-DMN connectivity should also interfere with the egocentric processing, resulting in a detrimental egocentric performance of DHH people.

In addition, spontaneous neural activity during rest is organized in multiple specific large-scale networks (Damoiseaux et al. 2006; De Luca et al. 2006; Fox and Raichle 2007). These intrinsic brain networks at rest may function as a potential 'scaffold' that undergoes subtle reconfigurations to form task-specific generative architectures (Smith et al. 2009; Cole et al. 2014, 2016; Tavor et al. 2016; Pezzulo et al. 2021). The changes in brain network configurations from rest to task states have been shown to predict individuals' task performance (Schultz and Cole 2016; Hearne et al. 2017; Alavash et al. 2019). In the present study, we also tried to investigate whether the DHH participants and the NH controls undergo an adaptive reconfiguration of intrinsic/resting-state large-scale networks during the transition from the resting state to the egocentric task.

Materials and Methods

In the current study, we re-analyzed the fMRI data from Li et al. (2022). Li et al. (2022) investigated the reorganization of large-scale brain networks extending beyond the auditory system. In the present study, however, we focused on the reorganization of large-scale brain networks involving the auditory system. Specifically, we investigated whether and how the reorganized connectivity between the auditory system, the DAN, the FPN, and the DMN contributes to the impaired egocentric processing in DHH people. Therefore, we targeted a different research question than Li et al. (2022). Given that the two studies share demographic information about the DHH participants and the NH controls and behavioral results, we will refer this information to Li et al. (2022) when appropriate.

Participants

Please see Li et al. (2022) for detailed demographic information on both subject groups. Briefly, twenty-six right-handed early DHH individuals (12 males; 21.54 ± 2.06 years old, mean ± SD) and 24 right-handed demographic-matched NH controls (12 males; 21.58 ± 1.69 years old, mean ± SD) participated in this study. Only the DHH and NH participants who reported no subjectively experienced balance problems and no clinical diagnosis of vestibular dysfunction were tested in the present study. All DHH participants had congenital, profound bilateral hearing loss (> 90 dB, each ear), as determined by a standard pure-tone audiometry procedure at 500, 1000, 2000, and 4000 Hz. Hearing loss was due to genetic or pregnancy-related factors, like hereditary deafness or drug side effects. The DHH participants exhibited inconsistent speech comprehension, ranging from poor to good, even with hearing aids. Each DHH participant was proficient in Chinese Sign Language but had poor speech articulation. The NH controls were native Chinese speakers who had no prior hearing problems. All participants had normal or corrected-to-normal vision, no color vision impairment, and no psychiatric or neurological diseases. Each participant had signed informed consent following the Helsinki Declaration before the experiment and got paid afterward. The Ethics Committee of the Department of Psychology, South China Normal University, approved this research.

Experimental Design

The experimental procedure was controlled using the Presentation software (Neurobehavioral Systems, RRID: SCR_002521, https://www.neurobs.com/). The stimuli consisted of a fork lying on an orange plate displayed on a gray background (Fig. 1A). The luminance of the fork was either dark (RGB: 64, 64, 64) or light (RGB: 192, 192, 192) gray. The width of the fork end was 2.5° of the visual angle, and the diameter of the plate was 15° of the visual angle. The fork was located at four different egocentric positions relative to the midsagittal line of the observer's own body (i.e., -2.67°, -1.7°, 1.7°, and 2.67°) and meanwhile at four different allocentric positions relative to the midsagittal line of the plate (i.e., -3.6°, -2°, 2°, and 3.6°). The two types of positions were orthogonally crossed. At each of the four egocentric locations of the fork, the background plate was moved around the fork, forming four different allocentric positions (Fig. 1A). The visual angles of the egocentric and allocentric positions of the targets were set via an initial psychophysical test using a different group of NH individuals to balance the task difficulty between the allocentric and egocentric judgments in the NH controls. Our previous studies demonstrated that these selected allocentric and egocentric positions effectively balanced the task difficulty across the three experimental tasks in the NH participants (Liu, Li, et al. 2017; Li et al. 2022).

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All participants performed three different tasks on the same set of stimuli, including the egocentric judgment task (EGO), the allocentric judgment task (ALLO), and the non-spatial luminance discrimination task (i.e., high-level baseline, HLB). In the egocentric task, individuals judged whether the fork was on the left or right side of their bodies' midsagittal plane. In the allocentric task, individuals judged whether the fork was on the left or right side of the plate's midsagittal plane. For these two spatial tasks, participants had to press the left button box with their left thumb for the response of the 'left-side' and the right button box with their right thumb for the response of the 'right-side'. In the non-spatial HLB task, individuals judged the luminance of the fork (dark gray or light gray) by pressing the left button box with their left thumb or the right button box with their right thumb. The mapping between the luminance and response hand was counterbalanced across participants. The experimental design was a 2 (between-subject factor: DHH vs. NH) × 3 (within-subject factor: ALLO, EGO, and HLB) two-factorial design.

In this study, a mixed fMRI design was used. Three types of tasks were presented as alternating task blocks with pseudo-random order, and an event-related design was embedded in each task block (Fig. 1B). All participants alternately performed these three types of tasks 10 times without any rest block. A pseudo-random order rather than a random order of all the task blocks ensured that the maximum time interval between any two identical blocks did not exceed 200 s, thereby meeting the high-pass filter of 1/200 Hz for the following processing of the task-state fMRI data. At the beginning of each block, a 3.3 s instruction was displayed to indicate the task of the upcoming block. Within each task block, 16 task trials and 6 null trials (only a blank default screen) were randomly mixed with the inter-trial intervals jittered from 1.4 s to 2.4 s in 250 ms steps. The target in each trial was presented for 250 ms (Fig. 1B). Such a short stimulus duration was used to minimize eye movements (Findlay 1997). The entire experiment included 160 experimental trials for each type of task and 180 null trials. Notably, no central fixation cross was presented throughout this experiment to avoid participants using it, rather than the task-required body's midsagittal plane, as an allocentric reference object to perform the egocentric task. Participants were also asked to keep their eyes straight ahead and not move their eyeballs. Our previous research using eye-tracking technology in a comparable experimental paradigm found that central fixation could be maintained equally well in the allocentric and egocentric tasks (Chen et al. 2012). Before the formal fMRI experiment, each participant underwent a training procedure to become familiar with the experimental tasks.

Data Acquisition

The imaging data were collected using a SIEMENS 3.0T Trio Tim system with a 32-channel head coil at the Institute of Psychophysics, Chinese Academy of Sciences, Beijing. First, resting-state images were acquired using a T2-weighted EPI sequence with 200 functional volumes. The corresponding parameters as follow: slice thickness = 3 mm, repetition time = 2200 ms, echo time = 30 ms, acquisition matrix = 64 × 64, flip angle = 90°, pixel size = $3.44 \times 3.44 \times 3.0$ mm^3, slices = 36 with a 0.75 mm gap. This resting-state session lasted for 7.33 minutes. During this session, participants were asked to relax, stay awake with closed eyes, and think about nothing. A T2-weighted EPI sequence with 729 volumes was then used to acquire individual task-state images, and the scanning parameters were the same as the resting-state session. This task-state fMRI scanning had only one run and lasted for 26.73 minutes. Finally, high-resolution structural images were acquired using a 3D MPRAGE T1-weighted sequence with 144 volumes lasting 8.09 minutes. The corresponding parameters were: slice thickness = 1.33 mm, repetition time = 2530 ms, echo time = 3.37 ms, inversion time = 1100 ms, acquisition matrix = 256 × 192, flip angle = 7°, pixel size = $0.5 \times 0.5 \times 1.33$ mm^3.

Analysis of Structural MRI Data

To investigate whether and how the potential structural changes in the brain anatomy of the DHH individuals are associated with egocentric processing, we calculated surface-based cortical thickness for each participant using the CAT12 toolbox (http://www.neuro.uni-jena.de/cat/), which is a well-established pipeline in the SPM12 software (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/) running on MATLAB R2019a. Subsequently, the between-group difference was tested, and the correlation analysis between the cortical thickness and the egocentric performance was performed for each group.

Specifically, individual structural MRI (sMRI) images were corrected for bias field and then segmented into grey matter, white matter, and cerebrospinal fluid. The projection-based thickness method was then used to estimate the cortical thickness (Dahnke et al. 2013), and a 15mm full-width/half-maximum Gaussian kernel was used to smooth the established central surfaces. An automated quality check and further visual inspection were performed, and all structural images passed through the quality control protocol. The between-group difference in the cortical thickness was tested using the full factorial design via the CAT12. Here, a less conservative threshold with a cluster level of $p < 0.05$ (uncorrected) and a standard voxel level of $p < 0.005$ (uncorrected) was used to identify structural changes in the DHH participants since no group differences were observed at a more conservative threshold of $p < 0.05$, FWE correction for multiple comparisons at the cluster level with a standard voxel level of $p < 0.005$ (uncorrected). Further, we calculated the Pearson correlation between the mean cortical thickness in the anatomical regions with structural alterations and the individual egocentric performance in each group of participants. Because we targeted the specific effect of the egocentric performance rather than the general effect of response speed, the relative reaction time (RT) difference between the egocentric and allocentric tasks ("EGO_RT – ALLO_RT") was used as the behavioral index for the egocentric performance in each participant. In this way, the general response speed in a single participant, which manifests in both the egocentric and allocentric tasks, was canceled out. For demonstration purposes, the thickness values of regions with structural alterations were shown as a function of the two groups, and no further statistical tests were performed to avoid the problem of double-dipping (Kriegeskorte et al. 2009, 2010).

Network Nodes Definition

Preprocessing of the task-state fMRI data

Task-state fMRI data were preprocessed using SPM12 software. The preprocessing included the following steps: 1) removing the first five volumes to ensure the data were collected when the magnetic field was stable and that participants had adapted to the scanning environment, 2) realigning the functional images to the new first volume to correct head movements, 3) normalizing all images to standard MNI152 space and resampling voxel size to 3 × 3 × 3 mm^3, and 4) smoothing with a 6mm full-width/half-maximum to alleviate the anatomical variability between participants.

Statistical Analysis

Preprocessed data were high-pass filtered at 1/200 Hz and modeled with a general linear model (GLM) in SPM12. The temporal autocorrelation was modeled using an AR(1) process. The GLM was used to construct a multiple regression design matrix at the individual-level analysis. Three types of target trials (ALLO, EGO, and HLB) were modeled in an event-related analysis. The three types of neural events were time-locked to the onset of the target trials by a canonical HRF and its first-order time derivative with an event duration of 0 s. Besides, the instructions, the invalid trials (missed, error, and outliers), and the six head movement parameters were modeled as another regressor of no interest. The null trials were not modeled and treated as the implicit baseline in the GLM model. Parameter estimates were calculated for each voxel using weighted least squares to provide maximum likelihood estimators based on the temporal autocorrelation of the data. For each participant, simple main effects for the three experimental conditions were computed and taken to a group-level analysis. Specifically, at the group-level analysis, two factors were included in a full factorial model with one task type factor (ALLO, EGO, and HLB) and one group factor (DHH vs. NH). To test whether the cross-modal reorganization occurred in the auditory system of the DHH participants' brains, a *t*-test contrast of "DHH (ALLO + EGO + HLB) > NH (ALLO + EGO + HLB)", collapsed over all three visual tasks, was established. In this way, the reorganized regions that displayed significantly elevated neural activity during the three visual tasks in the DHH than the NH group were included. To further test whether the neural interactions between the auditory cortex and the task-related regions were altered in the DHH participants' brains, an *F*-test contrast of "the main effect of tasks", i.e., "ALLO vs. EGO vs. HLB", collapsed over the two groups, was established. In this way, the brain regions that showed differential (positive and negative) activation between the three tasks were included. Areas of activation were identified as significant if they passed a threshold of $p < 0.005$, FWE correction for multiple comparisons at the cluster level with an underlying voxel level of $p < 0.001$ (uncorrected). The localized task-related regions, together with the reorganized auditory cortex, were combined to form a brain mask, and each voxel of this mask was considered a node in the subsequent modularity analyses. For demonstration purposes, mean parameter estimates were extracted from the reorganized clusters and displayed as a function of the two groups. No extra statistical tests were additionally performed on the extracted parameter estimates.

Modularity Analyses

Data Preprocessing

Resting-state fMRI data were preprocessed using the DPARSF module of the DPABI V6.0 software (http://rfmri.org/DPABI). The preprocessing included the following steps: 1) discarding the first five volumes, 2) slice timing correction, 3) head movement correction, 4) reorienting functional and structural images to achieve high-quality segmentation and normalization, 5) controlling for Friston-24 motion parameters, white matter signal, and cerebrospinal fluid signal as covariates, 6) normalizing functional images to standard MNI152 space using DARTEL and resampling voxel size to $3 \times 3 \times 3$ mm^3, and 7) bandpass filtering with 0.01-0.1 Hz. Given that removing the global signal would change the distribution of connectivity and increase negative correlations (Murphy et al. 2009; Liu, Nalci, et al. 2017; Murphy and Fox 2017), the global signal was not regressed out. The network node was each voxel in our pre-defined task mask. Hence, spatial smoothing, which would exaggerate the similarity between voxels, was not performed. The same preprocessing of the resting-state fMRI data was also applied to the task-state fMRI data to minimize the impact of preprocessing differences and ensure the comparability of modularity results between the resting-state and the task-state.

Network Construction

For the resting-state data, we extracted the whole time series of each voxel from our task mask and calculated the voxel-wise Pearson correlation matrix on the individual level, which was used to represent the edges of graph analysis. Notably, the task mask was used in the resting-state graph analysis to ensure that the same nodes were included as in the task-state graph analysis. For the task-state data, blocks with more than six error trials were discarded. Accordingly, four of the 26 DHH participants and four of the 24 NH controls had removed task blocks. Specifically, for the DHH group, one ALLO block and one EGO block were discarded in one participant, and one EGO block was discarded in the other three participants. For the NH group, one ALLO block and one HLB block were discarded in two participants, one EGO block was discarded in one participant, and one HLB block was discarded in one participant. There were 16 experimental trials in each task block. Therefore, for the DHH group, four EGO blocks (i.e., 4*16=64 EGO trials, 1.54%) in total and one ALLO block (i.e., 16 ALLO trials, 0.38%) in total were discarded across all the DHH participants. For the NH group, one EGO block (i.e., 16 EGO trials, 0.42%) in total, two ALLO blocks (i.e., 2*16=32 ALLO trials, 0.83%) in total, and three HLB blocks (i.e., 3*16=48 HLB trials, 1.25%) in total were discarded across all the NH participants. Given the effect of hemodynamic delay, the first 4 volumes (8.8 s) were removed, and the 2 volumes (4.4 s) of the next block were included in each valid block (Mostofsky et al. 2009), so there were 20 time points per block. The time series of each voxel from our mask was extracted, and a voxel-wise Pearson correlation matrix was calculated within each valid block on the individual level. All correlation matrices for each participant's task were then averaged (Mostofsky et al. 2009; Liang et al. 2016), resulting in one correlation matrix for each task type in each participant. A set of sparsity thresholds (2% to 5% with a step of 1%, i.e., the ratio of the number of actual edges to the maximum possible number of edges) were selected to ensure the sparsity nature of the brain network and simultaneously remove weak correlations. Subsequently, edges in binary networks were defined by assigning the value of 1 to the connections that survived a given threshold and 0 to the other connections. Due to the controversial physiological meaning of the negative connections (Anderson et al. 2011; Schwarz and McGonigle 2011; Keller et al. 2013), negative correlations were assigned the value 0 and removed from further analyses (Liang et al. 2016; Sun et al. 2017; Sha et al. 2018; Guo et al. 2019; Sulpizio et al. 2020). Therefore, we focused on the positive connections in our analyses by setting the negative correlations to zero.

Evaluating Network Properties

The graph-based modularity analyses were conducted on the resultant brain graphs via the GRETNA V2.0 software (https://www.nitrc.org/projects/gretna/). In order to identify brain modules, sets of nodes that are highly associated with each other but less associated with other modular nodes, the modified greedy optimization algorithm (Fortunato 2010) was used in which the modularity (Q) was defined as:

$$\mathrm{Q} = \sum_{s=1}^{N_M} \left[\, l_s/L - \left(d_s/2L\right)^2 \right],$$

where N_M is the number of non-overlapping modules, l_s is the number of within-module links in the module s, L is the total number of links in the network, d_s is the sum of degrees for each node in the module s, and the degree is the number of links connected to a node (Guimerà and Amaral 2005). The modularity of a given network quantifies the extent to which the network can be subdivided into modules with higher within-module than between-module connections (Newman and Girvan 2004). In real-world networks, modularity typically falls in the range of 0.3~0.7 (Newman and Girvan 2004).

We first performed the individual-level modularity analysis based on each participant's brain graph for the resting-state fMRI data. Since the module number and membership varied among individuals even within the same group, a group-level modularity analysis (collapsed over the two groups) was also performed to obtain a general modular structure shared by all the participants. Specifically, a group brain graph was created by averaging the correlation matrices across all participants and then thresholding at each network sparsity threshold from 2% to 5% in a step of 1%. After the group-level modularity analysis, the adjusted mutual information (AMI) was estimated to measure the similarity of module structure between the two groups. Since the modular partitions were similar between the DHH and NH groups based on the AMI analysis (see ‘Results’), the modules of interest comprising the DAN, the FPN, the DMN, and the bilateral STG were selected from the group-level modularity analysis at the moderate network sparsity of 3%. The sparsity of 3% was chosen based on the quality of the module partition (Liang et al. 2016). The present study was specially designed to explore the functional connectivity between the auditory system, the DAN, the FPN, and the DMN. Therefore, precise and reasonable identification of the four modules is the rule of thumb for sparsity selection in the present study. Although the step size of sparsity change is only 1%, there are significantly various module partitions at the different sparsity thresholds. For example, the number of edges included in module identification between each 1% step is very different, i.e., 9830*(9830-1)/2*1%, where 9830 is the number of nodes in our study (Rubinov and Sporns 2010). Low sparsity levels will generate disconnected graphs where the networks become severely fragmented (Meunier et al. 2009; Power et al. 2011). In our case, at the sparsity of 2% (see ‘Results’), the DMN was divided into three separate modules, and the FPN was divided into two separate modules. On the other hand, higher sparsity levels will generate graphs with low modularity equivalent to a random graph where the different networks are merged into one module (Meunier et al. 2009; Power et al. 2011). In our case, at the sparsity of 4% and 5% (see ‘Results’), the auditory cortex and part/all of the DAN were identified as one single module, and the bilateral insular regions were merged with the FPN. Due to the inaccurate network partitions at the sparsity of 2%, 4%, and 5%, it was challenging to answer, for example, how the connectivity between the auditory system and the DAN was reorganized in the DHH brain when the two modules were fragmented into several sub-modules (at the sparsity of 2%) or when the two modules were (partly) mixed (at the sparsity of 4% and 5%). Thus, we did not conduct further analyses at the sparsity thresholds of 2%, 4%, and 5%. This approach follows most previous studies adopting graph theory analyses: only the sparsity level with the most precise and reasonable network partition was selected and entered into further analyses (e.g., Meunier et al. 2009; Gratton et al. 2012; Liang et al. 2016; Gordon et al. 2017; Sun et al. 2017; Yoo et al. 2019; Liu et al. 2020; Ma et al. 2020; Lei et al. 2022). Among the segmented modules at the sparsity of 3%, the DAN, the FPN, and the DMN modules were visually identified according to the Yeo-7 networks (Yeo et al. 2011), and the STG was visually identified based on the Automated Anatomical Labeling (AAL) template (Tzourio-Mazoyer et al. 2002). Based on the above identified modules, the network properties at the nodal and the modular levels were then calculated during the resting and the task state, respectively.

In this study, we focused on the reorganization of the between-module connectivity involving the STG in the DHH individuals. Accordingly, the participation coefficient (PC) across the four modules of interest (DMN, DAN, FPN, and STG) was calculated at the nodal level. Since we were interested in the alterations of the inter-module connectivity between the STG and each of the three task-related networks (DAN, FPN, and DMN), the PC was estimated only between any pair of two modules involving the STG. The PC reflects the ability of a node i to keep communication between its own module and the other modules, defined as:

$$\mathrm{PC}_i = 1 - \sum_{s=1}^{N_M} \left(\frac{k_{is}}{k_i}\right)^2 ,$$

where N_M is the number of non-overlapping modules (i.e., ‘2’ for the current analysis), k_{is} is the number of positive links between node i and module s, and k_i is the sum number of positive links of node i in the network (including two modules in the current analysis) (Guimerà and Amaral 2005). Therefore, if the links of node i are distributed across all modules, the node’s PC is close to one, and if the links of node i are within its corresponding module, the node’s PC is close to zero.

At the modular level, we also calculated the between-module connectivity (STG-DAN, STG-FPN, and STG-DMN) for each participant during both the resting state and the egocentric task by averaging the PC values across all nodes/voxels in the two modules belonging to the same pair of modules (Geerligs et al. 2015; Sadaghiani et al. 2015; Baum et al. 2017).

Statistical Analysis

For the node-wise analysis, the PC image file for each participant was created based on individual nodes' PC values, and the created images were then submitted to a group-level analysis in SPM12. More specifically, the two-sample t-test was implemented for the resting-state data, while the full factorial model with one task type factor (ALLO, EGO, and HLB) and one group factor (DHH vs. NH) was implemented for the task-state data. During the task-state modularity analyses, we were particularly interested in the altered inter-module connectivity between the STG and the task-related networks, specifically during the egocentric task in the DHH participants compared to the NH controls. Therefore, an exclusive masking procedure was performed to eliminate the potential contribution from the other task of no interest, i.e., the contrast "DHH EGO > NH EGO" was exclusively masked by the contrast "DHH ALLO > NH ALLO". More concretely, a mask was first built based on the contrast "DHH ALLO > NH ALLO" at a liberal threshold of uncorrected voxel level of $p < 0.05$. Then, we discarded those significant voxels in this mask from the brain activations related to the target contrast "DHH EGO > NH EGO". In this way, the voxels that showed an altered neural coupling during the allocentric task in the DHH group when compared to the NH group ($p < 0.05$, uncorrected at the voxel level) were excluded from the analysis, leaving the specific alteration of neural coupling during the egocentric task in the DHH participants. To investigate whether and how the inter-module connections would benefit or harm the egocentric processing, we built a new model with only the egocentric PC images for both groups of participants and with their egocentric performance ("EGO_RT – ALLO_RT") as a covariate. Areas of activation were identified as significant if they passed a threshold of $p < 0.05$, FWE correction for multiple comparisons at the cluster level with an underlying voxel level of $p < 0.05$ (uncorrected). For demonstration purposes, mean PC values were extracted from the significantly activated regions and shown as a function of the subject group. No further statistical tests were performed to avoid double-dipping. Behavior-related activation did not survive correction for multiple comparisons, but several meaningful subthreshold results merited further exploration. As such, an uncorrected threshold of $p < 0.05$ was used to identify a trend toward significant activation.

For the module-wise analyses, we aimed to investigate whether and how the modular reconfigurations (STG-DAN, STG-FPN, STG-DMN) occurred in the DHH participants and the NH controls from the resting state to the egocentric task. Within each subject group, paired *t*-tests, with Bonferroni correction, were adopted to test the difference in the module-level mean PC between the resting state and the egocentric task. Since we already statistically tested the between-group difference at the nodal level, to avoid double-dipping, we did not use a 2 (between-subject factor: DHH vs. NH) × 2 (with-subject factor: Rest vs. EGO) ANOVA, which incorporates the statistical tests of the between-group difference. Finally, to test whether the modular reconfigurations, from the rest to the egocentric task, were associated with the specific effect of individuals' egocentric performance, we calculated the correlation between the between-state changes in the module-level mean PC ("Rest – EGO") and the relative RTs of the egocentric task ("EGO_RT – ALLO_RT").

Results

Structural alternations in the DHH individuals' brain

Surface-based morphometry analyses showed increased cortical thickness in the left STG of the DHH individuals compared to the NH controls (Fig. 2A and Table 1A). Interestingly, a marginally significant correlation between the mean cortical thickness in the left STG and the individual egocentric performance was observed in the DHH participants, $r = 0.38$, $p = 0.056$, i.e., there was a significant trend that the thicker the left STG in a DHH individual, the slower her/his egocentric judgment (Supplementary Fig. 1). However, no significant correlation between the two factors was found in the NH participants ($r = 0.01$, $p = 0.956$).

Table 1. Structural alteration and functional reorganization in the STG of the DHH.

Region	Hemisphere	Peak MNI coordinate (mm)	*t*-Value	Ke (voxels)
(A) Structural alteration				
Superior temporal gyrus (STG)	L	-54, -14, 4	4.57	143
(B) Functional reorganization				
Superior temporal gyrus (STG)	R	63, -15, 3	6.67	379
	L	-42, -36, 12	5.47	265

DHH, deaf and early hard of hearing; L, left; R, right.

-------------------Insert Fig. 2 about here-------------------

Cross-modal responses to all the visual tasks in bilateral STG of the DHH individuals' brain

The bilateral STG was significantly activated in the neural contrast "DHH (ALLO + EGO + HLB) > NH (ALLO + EGO + HLB)", indicating that neural activity in the bilateral STG of the DHH participants' brains generally increased upon performing the current three visual tasks, compared to the NH controls (Fig. 2B and Table 1B).

Brain module identification

Via an *F*-test on the task-state fMRI data, we first localized the task-related brain network involved in the differential (positive and negative) activation between any two of the three visual tasks, collapsed over the two groups. An extensive brain network was thus localized, including the DAN, the FPN, and the task-negative DMN (Fig. 3A).

Subsequently, the localized task-related network, together with the bilateral STG activated by the three visual tasks in the DHH individuals (see Fig. 2B), were combined as a brain mask image for the subsequent modularity analyses on the resting-state fMRI data.

-------------------Insert Fig. 3 about here-------------------

Results of the modularity analyses on the resting-state data showed high modularity Q values across all the sparsity levels, either in each participant group or in all participants combined (all more than 0.3) (Fig. 3B), indicating that the modular structure was a non-random community (Newman and Girvan 2004). At each network sparsity threshold, the AMI (DHH vs. NH) ranged from 0.61 to 0.77, suggesting that the modular structure was stable and similar between the two groups (Vinh et al. 2010). The four modules of interest (STG, DAN, FPN, and DMN) could be reasonably identified for both groups at the 2% sparsity threshold (Supplementary Fig. 2A), and the modular partitions, particularly the four modules of interest, were the most similar between the two groups at the sparsity threshold of 2%, through both visual inspection and the value of similarity index —AMI (0.77). At the other three sparsity thresholds (3%, 4%, and 5%), the AMI values were 0.71, 0.61, and 0.71, respectively. However, there were easily noticeable differences in the STG and the DAN modules between the two groups at the disparity thresholds of 3%-5% (Supplementary Fig. 2B-D). Although the four modules of interest were very similar between the two groups and were well separated at the sparsity of 2% (Supplementary Fig. 2A), they were not 100% identical between the two groups. For example, the bilateral insular regions were merged into the FPN in the NH group, which was not the case in the DHH group (see lateral yellow regions in Supplementary Fig. 2A). Due to the between-group difference in the nodes and edges of the modular partitions, one cannot use the specific modular partitions within the two groups to explore the between-group differences in the inter-module connectivity. Considering the imperative use of identical modules for a fair comparison of inter-module connectivity between the two groups, we adopted the module partitions based on the group-level brain graph (collapsed over the two groups) to obtain a common modular structure. The results showed that the low sparsity threshold at 2% generated a disconnected graph, where the DMN and the FPN became fragmented (Fig. 3C). Rather, the modular partitions were precise and reasonable at the moderate sparsity threshold of 3% (Fig. 3D). The higher sparsity thresholds at 4% and 5% generated graphs with low modularity equivalent to a random graph, where the STG and part/all of the DAN were merged into one single module (Fig. 3E-F). These findings are consistent with previous evidence (Meunier et al. 2009; Power et al. 2011).

Taken together, the modules identified explicitly within each group were most similar between the two groups and most reasonably separated at the sparsity of 2% (Supplementary Fig. 2A), while the modules identified across all the participants from both groups were precise and reasonable at the sparsity of 3% (Fig. 3D). This phenomenon mainly results from the different sample sizes in the two analyses: the within-group analyses are based on smaller sample sizes (around 20) than the analysis for both groups combined (over 40). When the number of participants is smaller, connections with low values in the average functional connectivity matrix are more likely to be spurious connectivity, potentially arising as a mere by-product of the noise in neural data (van Wijk et al. 2010; Fornito et al. 2012; van Den Heuvel and Fornito 2014; van den Heuvel et al. 2017). Therefore, a more stringent sparsity threshold (2% in the present study) was necessary to identify the high and real brain connections and remove the noisy connections to identify accurate modular structures within each group of participants. In contrast, the average correlation matrix obtained from a larger number of participants can mitigate the potentially noisy connections (Roberts et al. 2017; Betzel et al. 2019). Moreover, a larger sample size enables connectivity detection with more precision and reliability (Helwegen et al. 2023). Accordingly, a moderate sparsity threshold (3% in the present study) and more valid connections were sufficient to detect the accurate modular structure when the two groups of participants were combined. Therefore, the module partitions based on the group-level brain graph (collapsed over both groups of participants) were selected at the moderate network sparsity of 3% for further analyses (Fig. 3D). Specifically, ten modules in total were identified for all participants, and four of them (STG, DAN, FPN, and DMN) were selected for the subsequent graph-based analyses on both the resting-state and the task-state data.

Please note that common networks of interest (STG, DAN, FPN, and DMN) between the two groups were also derived via conjunctions between the modular partitions at the same sparsity threshold of 2% within each subject group (Supplementary Fig. 3A). The overlapped networks of interest between the two groups were then used to carry out the validation modular analyses to test the reliability of our findings further. The validation analysis replicated the major results based on the group-level (collapsed across both groups) masks. Please see the supplementary material for more information.

The resting state: increased module connectivity between the STG, the DAN, and the FPN in the brain of DHH individuals

For the resting-state data, the between-group difference in the pair-wise connectivity between the STG and the three task-related networks (the DAN, the FPN, and the DMN) was calculated at the nodal level.

Stronger inter-module connectivity between the STG and the DAN was observed in the DHH compared to the NH group (Fig. 4A). Specifically, the right middle occipital gyrus (MOG) extending to the bilateral superior parietal lobe (SPL) and the precuneus within the DAN exhibited significantly higher PC values with the bilateral STG in the DHH than NH group (Fig. 4A, left panel; and Table 2A). Moreover, the bilateral STG exhibited significantly higher PC values with the DAN in the DHH than the NH group (Fig. 4A, right panel; and Table 2A). Besides the DAN, the right inferior frontal gyrus (IFG) in the FPN showed significantly higher PC values with the STG in the DHH than the NH group (Fig. 4B and Table 2B). Taken together, the STG of the DHH showed increased connectivity with sub-regions both in the DAN and the FPN during the resting state.

Table 2. Participation coefficient (PC) results between the STG, the DAN, and the FPN during the resting state.

Region	Hemisphere	Peak MNI coordinate (mm)	*t*-Value	Ke (voxels)
(A) PC between STG and DAN				
DAN→STG (DHH > NH)				
Middle occipital gyrus (MOG)	R	30, -78, 24	4.81	449
Precuneus	*R*	*21, -63, 24*	*4.12*	
Cuneus	*L*	*-12, -75, 39*	*3.93*	
Superior parietal lobe (SPL)	*R*	*21, -60, 69*	*3.73*	
STG→DAN (DHH > NH)				
Superior temporal gyrus (STG)	R	57, -24, 9	5.03	60
	L	-54, -30, 9	3.50	42
(B) PC between STG and FPN				
FPN→STG (DHH > NH)				
Inferior frontal gyrus (IFG)	R	51, 15, 30	3.28	80

Italics indicate the coordinates of relevant local maxima within each significant cluster. DAN, dorsal attention network; FPN, frontoparietal network; DHH, deaf and early hard of hearing; NH, normal hearing; L, left; R, right.

-------------------Insert Fig. 4 about here-------------------

The task state: enhanced module connectivity between the STG and the task-related networks during the egocentric task in the brain of DHH individuals

For the task-state data, at the nodal levels, we aimed to investigate the between-group difference (DHH vs. NH) in the inter-module connectivity between the STG and the task-related networks (i.e., DAN, FPN, and DMN), especially during the egocentric task.

Compared to the NH group, we found enhanced connectivity between the STG and sub-regions of the DAN in the DHH group, specifically during the egocentric task (Fig. 5). More concretely, within the DAN, the right MOG extending into the precuneus showed significantly higher PC values with the STG in the DHH group compared to the NH group, especially during the egocentric task, rather than the allocentric task (Fig. 5A, the left panel; and Table 3A). Moreover, results from the behavior-related model showed that the PC value from the right MOG to the STG was significantly negatively correlated with the individual egocentric performance only in the DHH group but not in the NH group: the stronger the right MOG-STG connectivity in a DHH individual, the faster her/his egocentric judgment (Fig. 5A, the right panel). On the other hand, the right STG also showed significantly larger PC values with the DAN in the DHH than the NH group, especially in the egocentric task, rather than the allocentric task (Fig. 5B and Table 3A).

Table 3. Participation coefficient (PC) results between the STG, the DAN, the FPN, and the DMN during the task state.

Region	Hemisphere	Peak MNI coordinate (mm)	*t*-Value	Ke (voxels)
(A) PC between STG and DAN				
DAN→STG				
(DHH EGO > NH EGO) exclusively masked by (DHH ALLO > NH ALLO)				
Precuneus	R	9, -63, 39	3.40	96
Middle occipital gyrus (MOG)	*R*	*33, -72, 15*	*3.15*	
STG→DAN				
(DHH EGO > NH EGO) exclusively masked by (DHH ALLO > NH ALLO)				
Superior temporal gyrus (STG)	R	51, -27, 6	3.38	50
(B) PC between STG and FPN				
FPN→STG				
(DHH EGO > NH EGO) exclusively masked by (DHH ALLO > NH ALLO)				
Middle frontal gyrus (MFG)	R	45, 9, 42	4.71	162
Inferior parietal lobe (IPL)	R	45, -54, 51	4.07	114
Superior frontal gyrus (SFG)	R	24, 15, 63	3.58	68
STG→FPN				
(DHH EGO > NH EGO) exclusively masked by (DHH ALLO > NH ALLO)				
Superior temporal gyrus (STG)	R	60, -24, 9	4.00	60

	L	-60, -27, 9	3.66	44
(C) PC between STG and DMN				
DMN→STG				
(DHH EGO > NH EGO) exclusively masked by (DHH ALLO > NH ALLO)				
Cuneus	R	12, -57, 21	3.86	78
Precuneus	*M*	*3, -60, 30*	*3.28*	
Medial prefrontal cortex (mPFC)	M	9, 45, -12	3.21	51
STG→DMN				
(DHH EGO > NH EGO) exclusively masked by (DHH ALLO > NH ALLO)				
Superior temporal gyrus (STG)	R	60, -27, 6	3.19	39

Italics indicate the coordinates of relevant local maxima within each significant cluster. DAN, dorsal attention network; FPN, frontoparietal network; DMN, default-mode network; ALLO, allocentric task; EGO, egocentric task; DHH, deaf and early hard of hearing; NH, normal hearing; L, left; R, right.

------------------Insert Fig. 5 about here------------------

Besides the DAN, enhanced inter-module connectivity between the STG and the FPN, specifically during the egocentric task, was also found in the DHH rather than the NH group (Fig. 6). The right MFG, right IPL, and right SFG within the FPN exhibited significantly stronger PC values with the STG in the DHH than NH group especially in the egocentric task, rather than the allocentric task (Fig. 6A, the left panel; and Table 3B). Moreover, results from the behavior-related model showed that the PC value from the right MFG to the STG was significantly negatively correlated with the individual difference in the egocentric performance only in the DHH group but not in the NH group: the stronger the right MFG-STG connectivity in a DHH individual, the faster her/his egocentric judgment (Fig. 6A, the right panel). On the other hand, the PC values from the bilateral STG to the FPN were also significantly higher in the DHH than the NH group, specifically during the egocentric task, rather than the allocentric task (Fig. 6B and Table 3B).

------------------Insert Fig. 6 about here------------------

The task state: enhanced module connectivity between the STG and the DMN during the egocentric task in the DHH individuals' brain

For the inter-module connectivity between the STG and the DMN, the neural coupling was significantly higher in the DHH than the NH group, only during the egocentric rather than allocentric task (Fig. 7). Specifically, the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC) in the DMN exhibited significantly larger PC values with the STG in the DHH than the NH group, especially during the egocentric rather than allocentric task (Fig. 7A, the left panel; and Table 3C). Interestingly, results from the behavior-related model showed that the PC value from the PCC to the STG was significantly positively correlated with the individual difference in the egocentric performance only in the DHH group, but not in the NH group: the stronger the PCC-STG connectivity in a DHH individual, the slower her/his egocentric judgment (Fig. 7A, the right panel). On the other hand, the right STG also showed significantly larger PC values with the DMN in the DHH than the NH group during the egocentric rather than allocentric task (Fig. 7B and Table 3C).

-------------------Insert Fig. 7 about here-------------------

Lack of flexibility in network reconfiguration from rest to egocentric task in the brain of DHH individuals

For the inter-module connectivity between the STG and the FPN, the NH controls showed a significant decrease when the brain state transitioned from the rest to the egocentric task, $t = 4.91$, $p < 0.001$ (Fig. 8A, right). The DHH group, however, did not show such network reconfiguration, $t = 1.07$, $p = 0.30$ (Fig. 8A, left). For both the STG-DAN (Fig. 8B) and the STG-DMN (Fig. 8C) pairs, the inter-module connectivity was comparable between the resting state and the egocentric task in both the DHH group and the NH controls, all $ps > 0.1$. Besides, no significant correlation was found between the modular reconfiguration and the individuals' egocentric performance in either group, all $ps > 0.1$.

-------------------Insert Fig. 8 about here-------------------

Discussion

Body-centered visuomotor transformation during egocentric judgments is impaired after early auditory deprivation (Li et al. 2022). This behavioral impairment is associated with increased inter-network connectivity beyond the auditory system, particularly between the DMN and the task-relevant networks in the DAN and FPN (Li et al. 2022). It remains unknown, however, whether and how the large-scale reorganization involving the auditory cortex is associated with impaired egocentric spatial processing after early auditory deprivation. Here, we investigated the cross-modal reorganization in the auditory cortex of DHH people during body-centered visuomotor transformation focusing on altered neural network dynamics between the auditory cortex in the bilateral STG, the task-critical networks in the DAN and FPN, and the DMN during the egocentric task, compared to the allocentric task.

Morphologically, we observed increased cortical thickness in the left STG of the DHH group (Fig. 2A). Previous surface-based morphometry studies with a relatively small sample size (less than sixteen participants per group) showed no significant difference in the cortical thickness of the auditory regions between the DHH and NH groups (Li et al. 2012; Hribar et al. 2014; Smittenaar et al. 2016). A recent meta-analysis did not provide any clear outcome (Manno et al. 2021). This lack of significant differences is likely because the cortical folds in the temporal lobe are inconsistent across individuals. Thus larger sample sizes may be required to detect temporal lobe thickness changes (Pardoe et al. 2012). Accordingly, two recent studies with larger sample sizes (thirty and fifty participants per group, respectively) showed that the cortical thickness of the STG increased in DHH relative to NH people (Kumar and Mishra 2018; McCullough and Emmorey 2020). Loss of sensory input produces comparatively mild effects on synapse development (Winfield 1981, 1983; Bourgeois et al. 1989; Bourgeois and Rakic 1996; Kral et al. 2005). Instead, the subsequent synaptic pruning with removing unnecessary synapses and neurons, which may be related to cortical thinning, is supported by sensory experiences (Bourgeois et al. 1989; Bourgeois and Rakic 1996; Yu et al. 2013; Faust et al. 2021). Accordingly, early auditory deprivation leads to inadequate synaptic pruning. Also, myelination is associated with cortical thickness (Sowell et al. 2004; Natu et al. 2019), and previous evidence has shown a decreased myelination both in auditory (Emmorey et al. 2003; Hribar et al. 2014; Karns et al. 2016) and visual deprivation (Winfield 1983). Furthermore, abnormal cortical thickness may be related to cortical malformation (Hyde et al. 2007; Hogstrom et al. 2012). In the tension-based theory, cortical folding can be explained by mechanical tension along axons, dendrites, and glial processes (Van Essen 1997). Early auditory deprivation may change the tonotopic organization of a DHH individual's brain, related to a thicker auditory cortex (for review, Hribar et al., 2020). Therefore, the increased cortical thickness of the auditory cortex in the DHH participants' brains might imply that the lack of early auditory input results in inadequate synaptic pruning, demyelination, and cortical malformation. The cortical thickness of the left STG in the DHH participants exhibited a trend of positive correlation with their egocentric performance (Supplementary Fig. 1), indicating that as the cortical thickness of the auditory cortex increases in the DHH participants, the impairments in egocentric processing may become more severe. Functionally, we found that the auditory cortex in bilateral STG of the DHH was generally hyper-activated during all three visual tasks, as compared to the NH controls (Fig. 2B). Early auditory deprivation alters an individual's interaction with the external environment, which leads to a striking functional reorganization in the auditory system. Accordingly, mounting empirical evidence shows that the 'deprived' auditory cortex of DHH people is recruited by the remaining senses, such as visual and vibrotactile stimuli (Bavelier et al. 2000, 2001; Fine et al. 2005; Karns et al. 2012; Cardin et al. 2013, 2018; Ding et al. 2015; Benetti et al. 2017, 2021).

Besides hearing loss, we cannot rule out the effects of sign-language experiences since all DHH participants in the present study were sign-language users. Sign language, a visuospatial language that exploits visual imagery, space, and movement (MacSweeney et al. 2008), has been shown to enhance an individual’s visuospatial representations (Emmorey 2002; Keehner and Gathercole 2007; Pyers et al. 2010). During a mental rotation task, researchers found that DHH and NH signers were faster for object rotation than NH non-signers (Emmorey et al. 1993). Previous studies suggest that objects are encoded in allocentric and egocentric reference frames, with the former predominating during mental rotation (Corballis et al. 1976, 1978). Therefore, signers’ enhanced mental rotation abilities may be related to a more critical reliance on the allocentric reference frame (Masataka 1995). Interestingly, a recent study found that as the proficiency of learned sign language increases, the superior lateral occipital cortex (LOC) exhibited a more robust connectivity with the high-level language region (i.e., IFG) during a sign-related semantic judgment task (Banaszkiewicz et al. 2021). The superior LOC codes visuospatial representations during allocentric judgments (Committeri et al. 2004; Zaehle et al. 2007; Chen et al. 2012). Therefore, the findings mentioned before imply that sign-language experiences might promote the dominance of the allocentric reference frame. Accordingly, we speculate that the egocentric reference frame might be compromised by the dominating allocentric reference frame in DHH people using sign language. Moreover, as sign language fluency increases, the allocentric reference frame might become more dominant, further impairing the function of the egocentric reference frame. To compensate for the impaired egocentric processing potentially caused by sign language use, the STG might become more integrated with the task-critical FPN during the egocentric task (Fig. 6). The effect of sign language on the cortical reorganization involving the STG remains controversial. Some researchers have found that sign language plays an essential role in the neural plasticity of the STG in the DHH (Neville et al. 1998; Petitto et al. 2000; Sadato et al. 2004; Cardin et al. 2013), an effect that could not be observed in other studies (Bavelier et al. 2001; MacSweeney et al. 2004; Fine et al. 2005; Olulade et al. 2014; Twomey et al. 2017). Therefore, sign language might explain some of the present results. Further research with DHH signers, NH signers, and NH non-signers is warranted to tease apart the effect of early auditory deprivation vs. sign-language experience on the large-scale functional reorganization of the auditory system during the egocentric task. Please also note that vestibular deficits have a high comorbidity rate with hearing loss (Moïn-Darbari et al. 2021). Moreover, the STG has been proven to be part of the vestibular cortical network (Bense et al. 2004; Dieterich and Brandt 2008, 2015; Helmchen et al. 2009; Lopez et al. 2012), and vestibular compensation has been associated with network reorganization involving the auditory system (Grosch et al. 2021). Although the DHH participants in the present study reported no subjectively experienced balance problems, they might have undetected vestibular impairment (Tamaki et al. 2021). Therefore, putative deficits of vestibular functions might explain some of the present results involving the STG. Further work will need to tease apart the effect of early auditory deprivation vs. vestibular deficits on the large-scale network reorganization underlying the impaired egocentric processing in the DHH people.

The functional cross-modal reorganization in the DHH is not only confined within the auditory system but also manifests as altered cortico-cortical connectivity between the auditory cortex and other cortical regions during a variety of visual tasks (Bavelier et al. 2000; Shiell et al. 2015; Benetti et al. 2017, 2021; Bola et al. 2017). It remains unclear, however, whether the altered neural network dynamics between the STG and other cortical areas were beneficial or detrimental to a specific visual task. In the present study, the auditory system in the bilateral STG showed enhanced functional connectivity with the DAN and the FPN in the DHH people (compared to the NH controls) during the resting state (Fig. 4) and the egocentric task (Figs. 5 and 6). Moreover, the stronger the functional connectivity during the egocentric task between the STG and the DAN and between the STG and the FPN, the better DHH persons performed in the egocentric task (Figs. 5A and 6A, the right panel). This finding indicates a beneficial role of enhanced STG-task network connectivity. Previous studies suggest that during the egocentric task, the DAN supports general visuospatial representations (Committeri et al. 2004; Chen et al. 2012, 2014; Gomez et al. 2014; Liu, Li, et al. 2017), while the FPN supports the body-centered visuomotor transformation

(Galati et al. 2000; Neggers et al. 2006; Chen et al. 2012, 2014; Liu, Li, et al. 2017). In order to ensure efficient task performance, the task-relevant regions are highly connected to maintain the high modularity of the task-relevant network; meanwhile, the task-relevant regions are disconnected from the task-irrelevant regions (Ekman et al. 2012; Gratton et al. 2016). In the present study, the STG was not involved in the egocentric task for the NH controls (Fig. 2B), i.e., a task-irrelevant area. Due to environmental noise, e.g., the scanner noise in the present fMRI study, the auditory system in the STG may even act as a distracting region during the egocentric task for the NH controls. Thus, to ensure efficient egocentric judgments, the task-critical FPN needs to be highly segregated/disconnected from the auditory system (Figs. 6 and 8A). For DHH individuals, however, both the reorganized auditory system in the STG and the task-relevant DAN and FPN were involved in the egocentric task (Figs. 2B and 3A). Therefore, the neural coupling between the STG, the DAN and the FPN was enhanced to optimize the egocentric performance: the higher the neural coupling, the better the egocentric performance in the DHH people (Figs. 5A and 6A, the right panel). Previous evidence suggests a beneficial role of increased functional connectivity between task-related networks during near-threshold perception (Weisz et al. 2014; Leske et al. 2015; Sadaghiani et al. 2015), visual attention (Spadone et al. 2015), and working memory (Braun et al. 2015; Shine et al. 2016). However, it remains unclear how such increased interaction between task-related networks impacts spatial reference frame tasks. In the present study, the STG of the DHH people showed increased connectivity with the task-related DAN and FPN during the egocentric task. The increased integration between task-related regions is crucial for recruiting necessary resources and optimizing widespread communications (Shine et al. 2016; Gonzalez-Castillo and Bandettini 2018; Menon and D’Esposito 2022). Accordingly, the efficient information flow between the STG and the cortical areas underlying the egocentric reference frame might facilitate body-centered visuomotor transformations, mitigating the impaired egocentric processing after early auditory deprivation.

On the other hand, the auditory cortex of the DHH group also showed enhanced connectivity with the task-irrelevant DMN during the egocentric task (Fig. 7). In contrast to the enhanced STG-task-relevant network connectivity, the enhanced STG-task-irrelevant DMN connectivity was associated with an impaired egocentric performance of the DHH people: the stronger the STG-DMN connectivity, the worse the egocentric performance in the DHH people (Fig. 7A, the right panel). The DMN is generally deactivated during various externally directed tasks to suppress task-irrelevant distractions (Shulman et al. 1997; Gusnard and Raichle 2001; Raichle et al. 2001; Fox et al. 2005). Therefore, a stronger anti-correlation between the DMN and the task-positive networks predicts better task performance (Sala-Llonch et al. 2012; Thompson et al. 2013). Furthermore, previous evidence shows that efficient task performance is associated with stronger modularity in the task-negative DMN in terms of lower between-module connectivity between the DMN and the task-relevant neural networks and higher within-module connectivity in the DMN (Weisz et al. 2014; Sadaghiani et al. 2015; Gonzalez-Castillo and Bandettini 2018). It has been suggested that the DAN and the FPN, two task-critical networks supporting the egocentric task, show stronger functional and structural connectivity with the DMN in DHH people (Dell Ducas et al. 2021; Li et al. 2022). Moreover, increased inter-network connectivity between the task-irrelevant DMN and the task-relevant DAN and FPN was associated with impaired egocentric performance in DHH people (Li et al. 2022). Given that the DHH participants' STG became more integrated with the task-relevant DAN and FPN to improve the egocentric processing (Figs. 5 and 6), the increased neural coupling between the task-relevant STG and the task-irrelevant DMN interfered with the egocentric processing, resulting in detrimental egocentric performance in the DHH people (Fig. 7).

To summarize, we revealed extensively reorganized inter-module connectivity between the auditory system in the bilateral STG, the task-relevant DAN and FPN, and the task-irrelevant DMN in the DHH people during body-centered visuomotor transformation. The STG in the DHH people becomes more integrated with the task-relevant regions in the DAN and FPN during the egocentric task. Accordingly, the more robust connectivity between the STG of DHH people and the task-relevant networks was associated with enhanced egocentric performance. In comparison, the stronger connectivity between the STG of DHH people and the task-negative DMN was associated with deteriorated egocentric performance.

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Figures

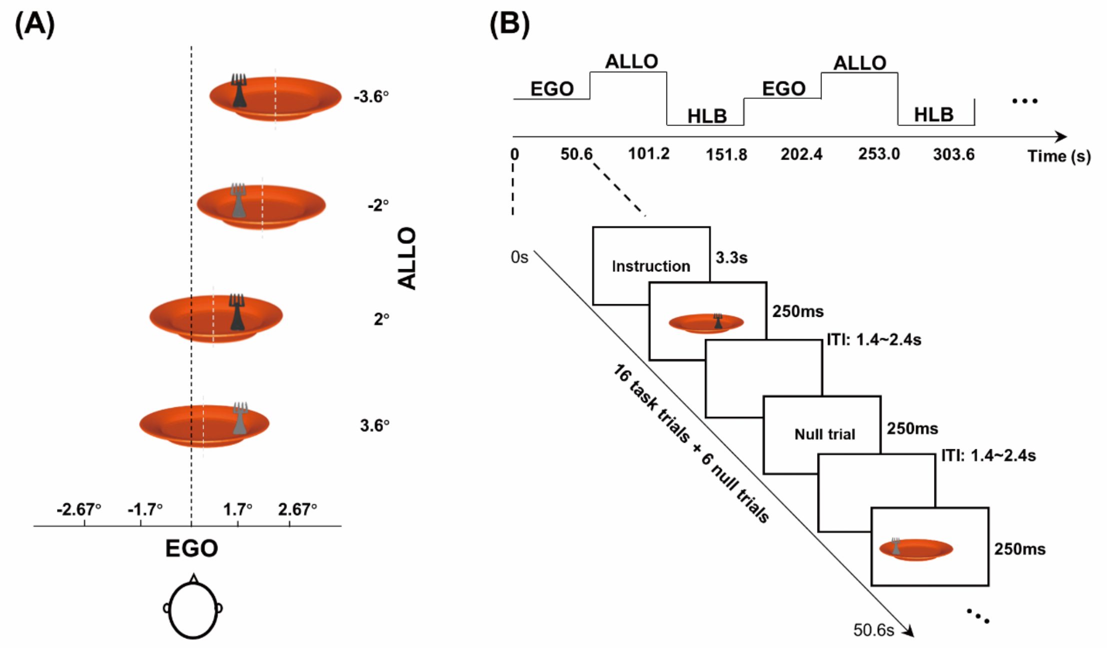


Figure 1. Stimuli and paradigm (adapted from Li et al., 2022). (A) Stimuli. The stimuli consisted of a fork lying on a plate. The luminance of the fork was either dark or light gray. The fork was located at 4 different egocentric positions (-2.67°, -1.7°, 1.7°, and 2.67°) relative to the midsagittal line of the observer's own body, i.e., the black vertical dashed line. Meanwhile, at each of the four egocentric locations of the fork, the background plate was moved around the fork, forming 4 different allocentric positions (-3.6°, -2°, 2°, and 3.6°) relative to the midsagittal line of the plate, i.e., the gray vertical dashed line. The egocentric and the allocentric positions were orthogonally crossed. (B) Paradigm. A mixed fMRI design was used. Three tasks were presented as alternating task blocks with pseudo-random order, and an event-related design was embedded in each task block. At the beginning of each block, a 3.3 s instruction was displayed to indicate the task of the upcoming block. In the egocentric task (EGO), participants were asked to judge the fork location relative to their bodies' midsagittal plane (left vs. right). In the allocentric task (ALLO), participants were asked to judge the fork location relative to the plate's midsagittal plane (left vs. right). In the high-level baseline task (HLB), participants were asked to judge the luminance of the fork (dark vs. light grey). Within each task block, sixteen task trials and six null trials (only a blank default screen) were randomly mixed with the inter-trial intervals (ITI) jittered from 1.4 s to 2.4 s in a step of 250 ms. The target in each trial was presented for 250 ms.

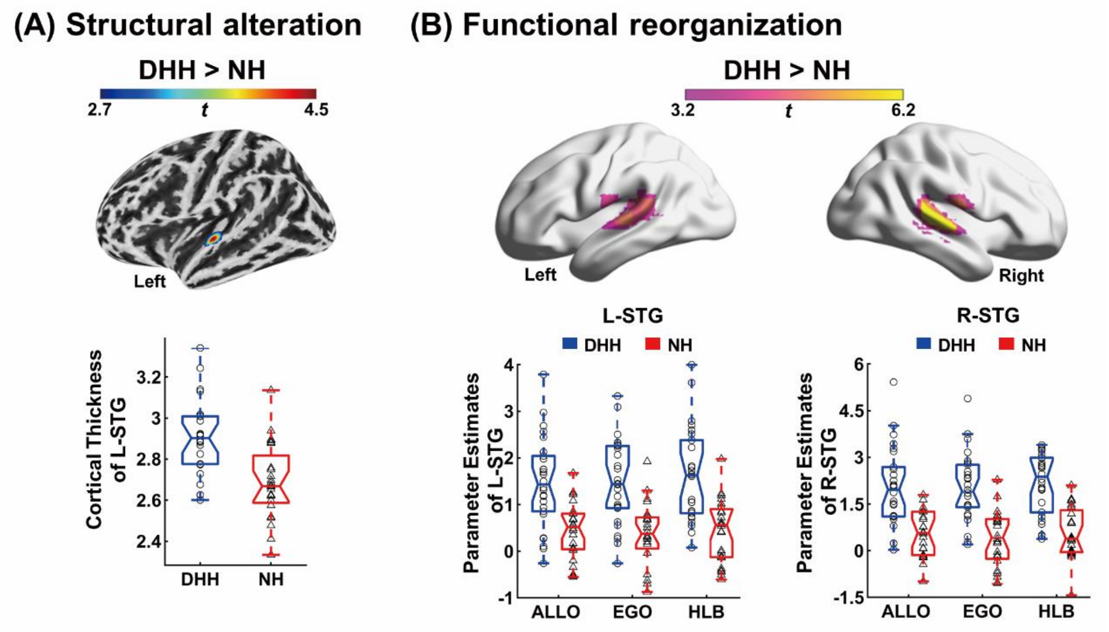


Figure 2. Structural alteration and functional reorganization in the brains of deaf and early hard of hearing (DHH) participants. (A) Structural alteration. The DHH group showed increased cortical thickness in the left superior temporal gyrus (STG) compared to the normal hearing (NH) controls. The box plot shows the mean thickness values in the area of structural change for each group. (B) Functional reorganization. Compared to the NH controls, the DHH participants showed significantly elevated neural activity in bilateral STG in all three visual tasks (ALLO, EGO, and HLB). The box plots show the mean amplitude of BOLD responses in each group's significantly activated regions in the three tasks. Note that all the box plots are shown only for demonstration purposes, and no further statistical tests were performed to avoid double-dipping. ALLO, allocentric task; EGO, egocentric task; HLB, high-level baseline task; L, left; R, right.

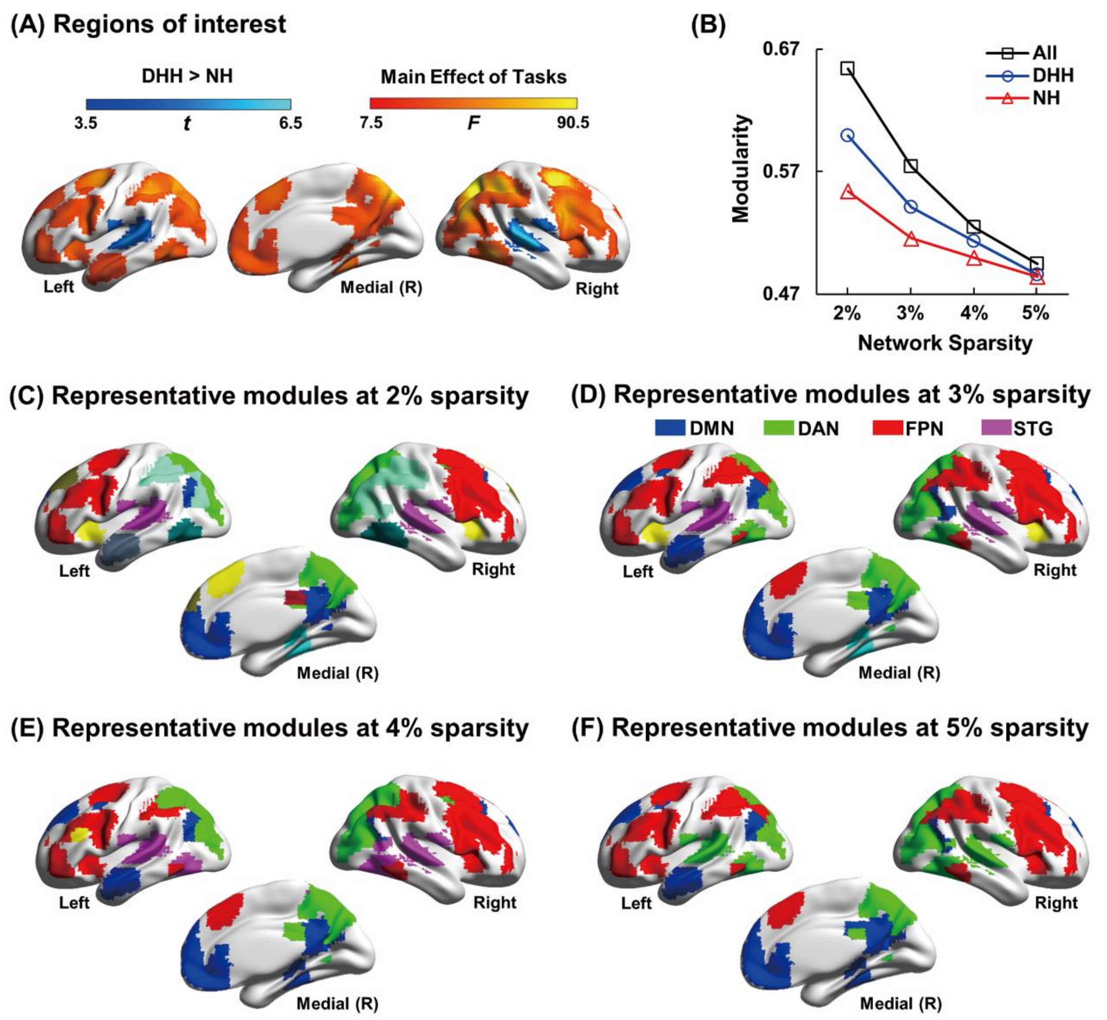
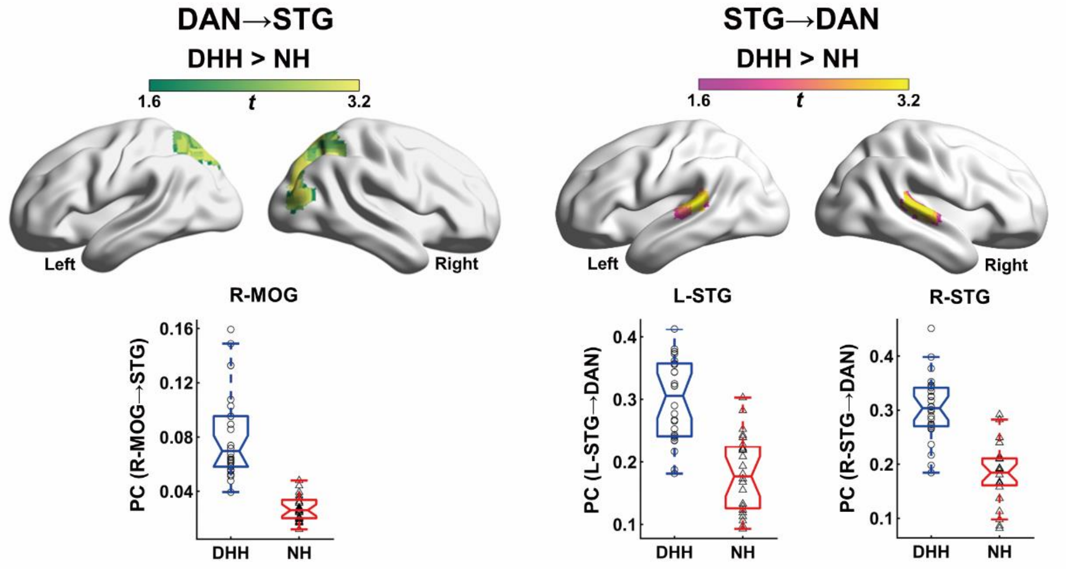


Figure 3. Module identification. (A) The brain mask used for module identification. The regions in warm colors are the brain regions that showed differential (positive or negative) activation between any two of the three tasks "ALLO vs. EGO vs. HLB" for both groups of participants. The regions in cold colors are the bilateral superior temporal gyrus (STG) that showed significantly elevated neural activity during the three visual tasks in the deaf and early hard of hearing (DHH) compared to the normal hearing (NH) group, i.e., "DHH (EGO + ALLO + HLB) > NH (EGO + ALLO + HLB)". (B) Mean modularity was obtained for the DHH group, the NH group, and all the participants (collapsed over the two groups), respectively, with the network sparsity from 2% to 5% based on the resting-state fMRI data. Maps of representative modules from the resting-state data of all participants at the sparsity thresholds of (C) 2%, (D) 3%, (E) 4%, and (F) 5% were shown, respectively. At the network sparsity of 3%, the default-mode network (DMN), the dorsal attention network (DAN), the frontoparietal network (FPN), and the STG were well separated. ALLO, allocentric task; EGO, egocentric task; HLB, high-level baseline task; R, right.

(A) PC between STG and DAN



(B) PC between STG and FPN

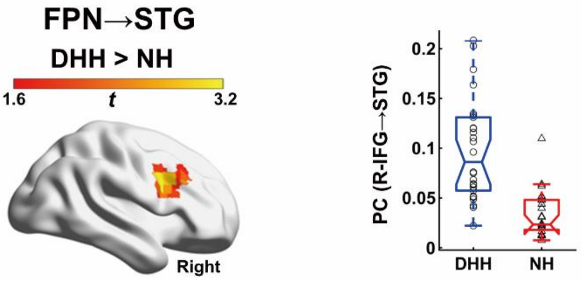


Figure 4. Resting-state results of module connectivity between the superior temporal gyrus (STG), the dorsal attention network (DAN), and the frontoparietal network (FPN). (A) Participation coefficient (PC) between the STG and the DAN. *Left panel*: The right middle occipital gyrus (MOG) extending to the bilateral superior parietal lobe (SPL) and the precuneus within the DAN exhibited significantly higher PC values with the STG in the deaf and early hard of hearing (DHH) than the normal hearing (NH) group during the resting state. *Right panel*: The bilateral STG exhibited significantly higher PC values with the DAN in the DHH than the NH group during the resting state. (B) The right inferior frontal gyrus (IFG) in the FPN exhibited significantly higher PC values with the STG in the DHH than the NH group during the resting state. For demonstration purposes, mean PC values were extracted from the significantly activated regions and shown as a function of the subject group. No further statistical analysis was performed on the extracted PC values to avoid double-dipping. L, left; R, right.

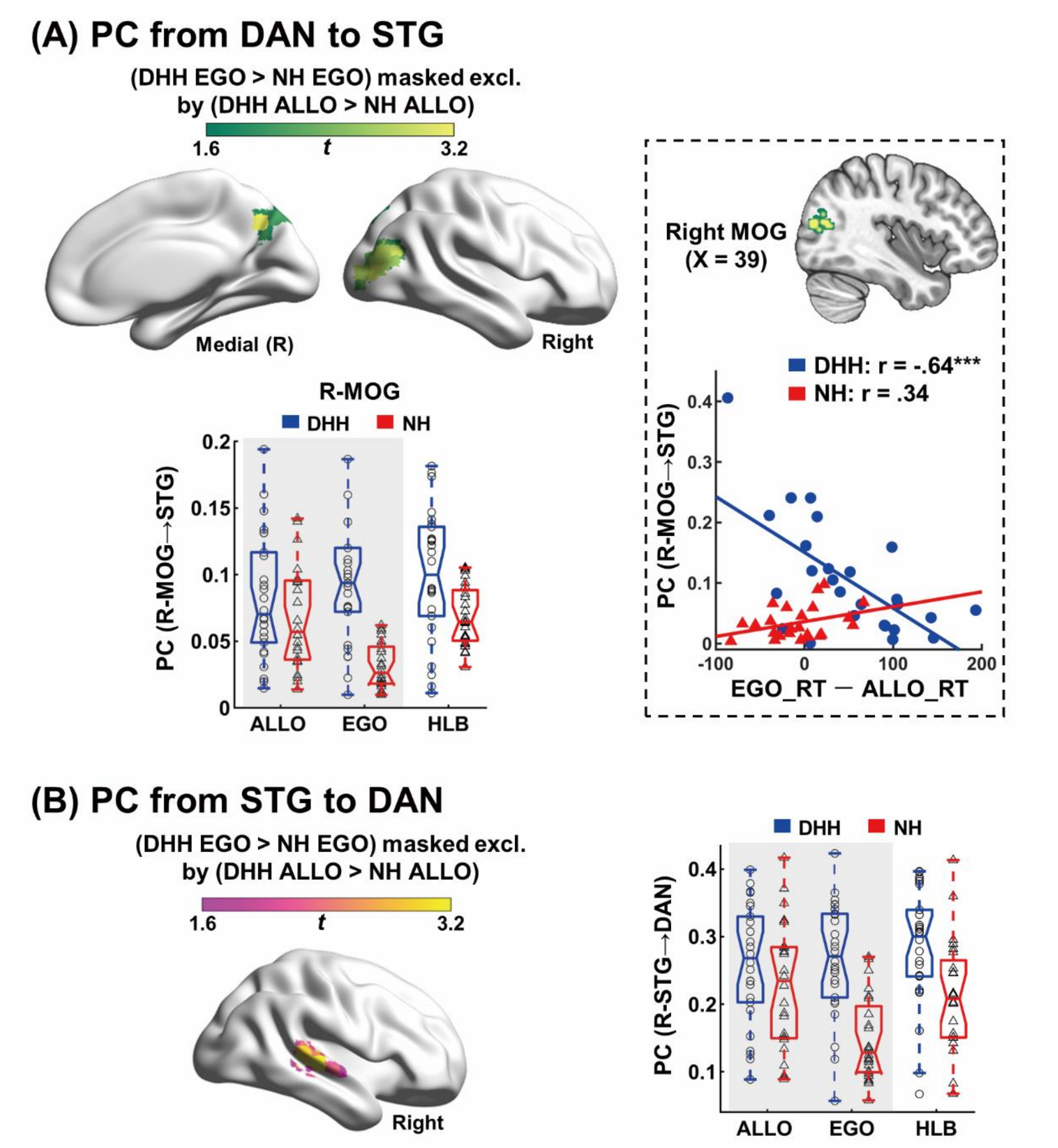


Figure 5. Task-state participation coefficient (PC) results between the superior temporal gyrus (STG) and the dorsal attention network (DAN). (A) PC from the DAN to the STG. *Left panel*: The interaction effect between the subject group (DHH vs. NH) and the visual tasks (EGO vs. ALLO). The right middle occipital gyrus (MOG) extending to the precuneus within the DAN exhibited significantly higher PC values with the STG in the DHH than the NH group, especially during the egocentric task rather than the allocentric task. Moreover, the PC value from the right MOG in the DAN to the STG was significantly negatively correlated with the egocentric performance ("EGO_RT – ALLO_RT") only in the DHH group but not in the NH group (*right panel*). The stronger the right MOG-STG connectivity in a DHH individual, the faster the egocentric judgment. ***: $p < 0.001$. (B) PC from the STG to the DAN. The right STG showed significantly larger PC values with the DAN in the DHH than the NH group, especially during the egocentric rather than the allocentric task. For demonstration purposes, mean PC values were extracted from the significantly activated regions and shown as a function of the subject group. No further statistical analysis was performed on the extracted PC values to avoid double-dipping. The conditions involved in the neural contrast were shaded. ALLO, allocentric task; EGO, egocentric task; HLB,

high-level baseline task; DHH, deaf and early hard of hearing; NH, normal hearing; L, left; R, right; RT, reaction time.

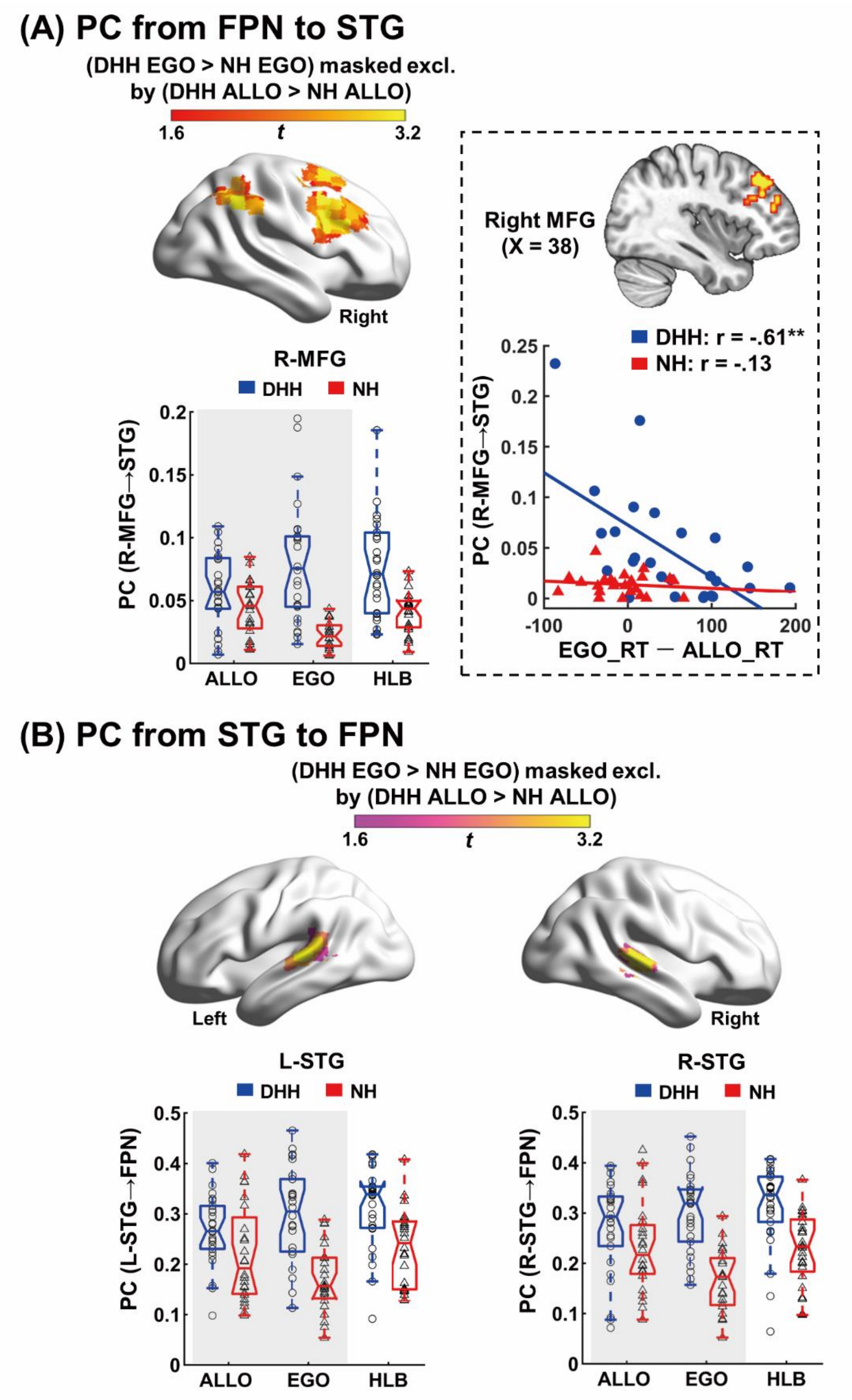


Figure 6. Task-state participation coefficient (PC) results between the superior temporal gyrus (STG) and the frontoparietal network (FPN). (A) PC from the FPN to the STG. *Left panel*: The

interaction effect between the subject group (DHH vs. NH) and the visual tasks (EGO vs. ALLO). Extensive areas in the FPN, including the right middle frontal gyrus (MFG), right inferior parietal lobe (IPL), and right superior frontal gyrus (SFG), exhibited significantly stronger PC values with the STG in the DHH than the NH group, especially during the egocentric rather than the allocentric task. Moreover, the PC value from the right MFG in the FPN to the STG was significantly negatively correlated with the egocentric performance ("EGO_RT – ALLO_RT") only in the DHH group but not in the NH group (*right panel*). The stronger the right MFG-STG connectivity in a DHH individual, the faster the egocentric judgment. **: $p < 0.01$. (B) PC from the STG to the FPN. The bilateral STG showed significantly larger PC values with the FPN in the DHH than the NH group, especially during the egocentric rather than the allocentric task. For demonstration purposes, mean PC values were extracted from the representative significantly activated regions and shown as a function of the three tasks in each subject group. No further statistical analysis was performed on the extracted PC values to avoid double-dipping. The conditions involved in the neural contrast were shaded. ALLO, allocentric task; EGO, egocentric task; HLB, high-level baseline task; DHH, deaf and early hard of hearing; NH, normal hearing; RT, reaction time; L, left; R, right.

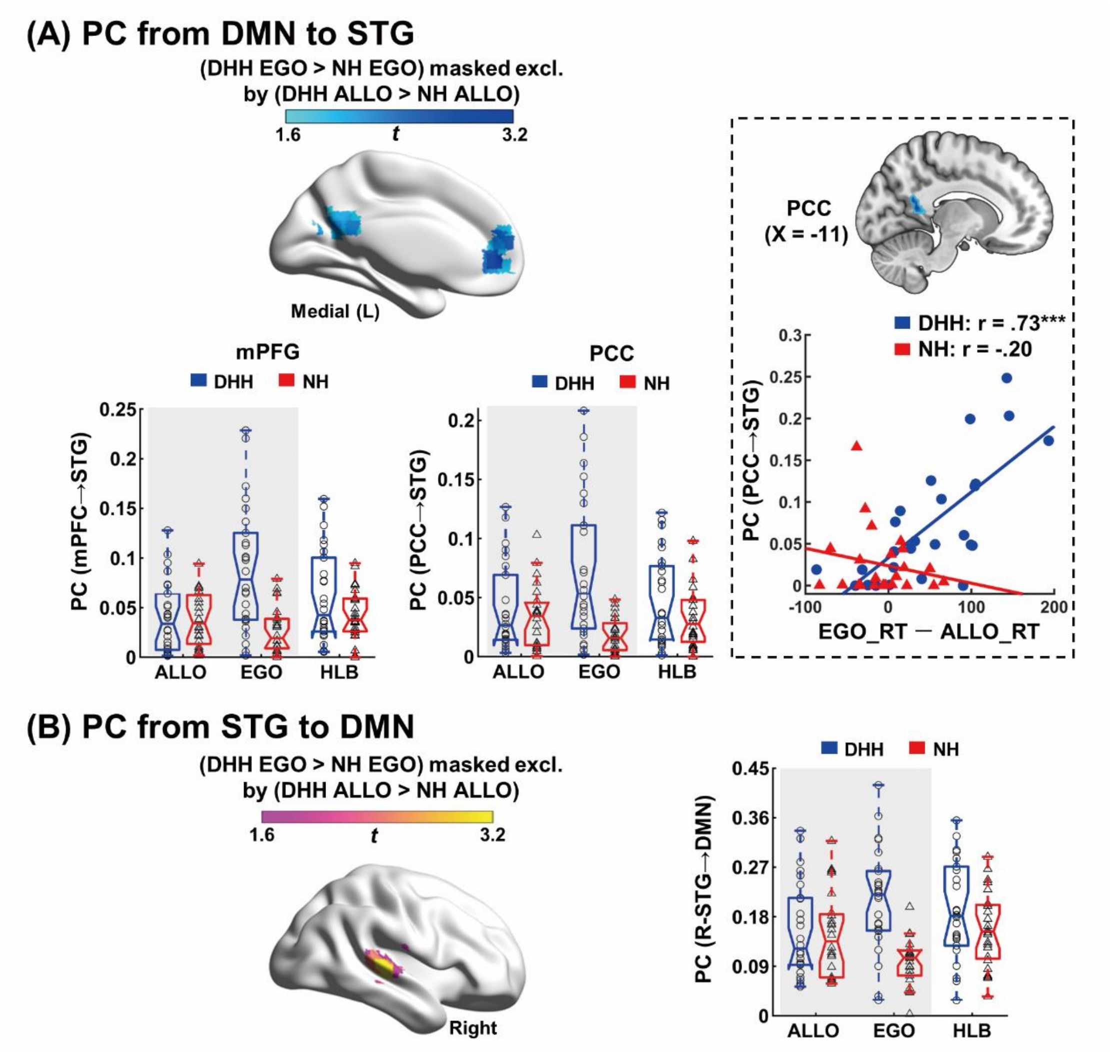


Figure 7. Task-state participation coefficient (PC) results between the superior temporal gyrus

(STG) and the default-mode network (DMN). (A) PC from the DMN to the STG. *Left panel*: The interaction effect between the subject group (DHH vs. NH) and the visual tasks (EGO vs. ALLO). Both the medial prefrontal cortex (mPFC) and the posterior cingulate cortex (PCC) in the DMN showed significantly stronger PC values with the STG in the DHH than the NH group, especially during the egocentric rather than the allocentric task. Moreover, the PC value from the PCC in the DMN to the STG was significantly positively correlated with the egocentric performance ("EGO_RT – ALLO_RT") only in the DHH group but not in the NH group (*right panel*). The stronger the PCC-STG connectivity in a DHH individual, the slower the egocentric judgment. ***: $p < 0.001$. (B) PC from the STG to the DMN. The right STG showed significantly stronger PC values with the DMN in the DHH than the NH group during the egocentric rather than allocentric task. For demonstration purposes, mean PC values were extracted from the significantly activated regions and shown as a function of the three tasks in each subject group. No further statistical analysis was performed on the extracted PC values to avoid double-dipping. The conditions involved in the neural contrast were shaded. ALLO, allocentric task; EGO, egocentric task; HLB, high-level baseline task; DHH, deaf and early hard of hearing; NH, normal hearing; RT, reaction time; L, left.

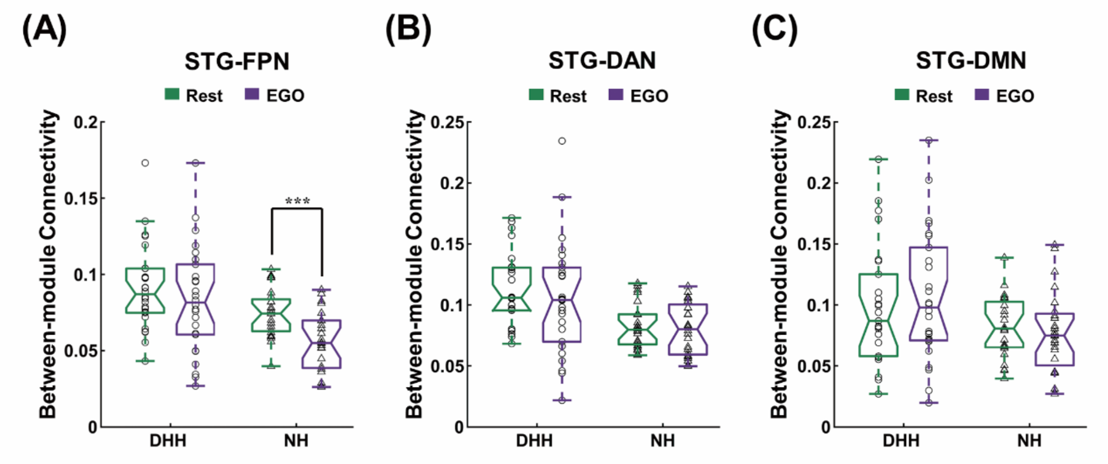


Figure 8. Alterations in between-module connectivity during the egocentric task relative to the resting state in the two subject groups. (A) STG-FPN. (B) STG-DAN. (C) STG-DMN. ***: $p < 0.001$. STG, superior temporal gyrus; FPN, frontoparietal network; DAN, dorsal attention network; DMN, default-mode network; EGO, egocentric task; DHH, deaf and early hard of hearing; NH, normal hearing.