

1 **Sensory experience modulates the reorganization of auditory**
2 **regions for executive processing**

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1 **Abstract**

2 Crossmodal plasticity refers to the reorganisation of sensory cortices in the absence of their
3 typical main sensory input. Understanding this phenomenon provides insights into brain function
4 and its potential for change and enhancement. Using fMRI, we investigated how early deafness
5 influences crossmodal plasticity and the organisation of executive functions in the adult human
6 brain. Deaf (N=25; age: mean=41.68, range=19-66, SD=14.38; 16 female, 9 male) and hearing
7 (N=20; age: mean= 37.50, range= 18-66, SD= 16.85; 15 female, 5 male) participants performed
8 four visual tasks tapping into different components of executive processing: task switching,
9 working memory, planning and inhibition. Our results show that deaf individuals specifically
10 recruit “auditory” regions during task switching. Neural activity in superior temporal regions,
11 most significantly in the right hemisphere, are good predictors of behavioural performance
12 during task switching in the group of deaf individuals, highlighting the functional relevance of
13 the observed cortical reorganisation. Our results show executive processing in typically sensory
14 regions, suggesting that the development and ultimate role of brain regions are influenced by
15 perceptual environmental experience.

16

1 Introduction

2 Sensory systems feed and interact with all aspects of cognition. As such, it is likely that
3 developmental sensory experience will impact the organisation of higher-order cognitive
4 processes such as executive functions. Here we studied executive processing in early deaf
5 individuals in order to understand the influence of early sensory experience on higher-order
6 cognition and neural reorganisation.

7 Executive functions are higher-order cognitive processes responsible for flexible and goal-
8 directed behaviours, which have been associated with activity in frontoparietal areas of the
9 brain.¹ However, studies on deafness have shown reorganisation for visual working memory in
10 regions typically considered to be part of the auditory cortex.²⁻⁵ These working memory
11 responses in auditory regions suggest that, in the absence of early sensory stimulation, a sensory
12 region can change its function as well as the perceptual modality to which it responds.^{6,7} The
13 adaptation of sensory brain regions to processing information from a different sensory modality
14 is known as crossmodal plasticity.⁷⁻¹⁹ In deaf individuals, crossmodal plasticity often refers to
15 responses to visual or somatosensory stimuli in regions of the superior temporal cortex which in
16 hearing individuals are typically involved in processing sounds^{7-11, 14-19}. The common
17 assumption here, and in general when referring to crossmodal plasticity, is that the auditory
18 cortex will preserve its sensory processing function, but process a different type of sensory input.
19 The presence of working memory responses in the auditory regions of deaf individuals takes the
20 concept of crossmodal plasticity further, suggesting that, in the absence of early auditory
21 stimulation, there is a shift from sensory to cognitive processing in such regions. If this is the
22 case, it would suggest that cortical functional specialisation for sensory or cognitive processing is
23 partially driven by environmental sensory experience. The aim of our study is to elucidate the
24 role of the auditory cortex of deaf individuals in executive functions, in order to understand how
25 sensory experience impacts cognitive processing in the brain. Specifically, we tested whether the
26 auditory regions of deaf individuals are involved in cognitive control or whether they have a role
27 in specific subcomponents of executive functions.

1 To address our aims, we conducted an fMRI experiment in deaf and hearing individuals.
2 Participants performed tasks tapping into different executive functions: switching, working
3 memory, planning, and inhibition. If the auditory cortex of deaf individuals has a role in
4 cognitive control, we would expect all tasks to recruit this region. However, if the auditory areas
5 of deaf individuals are involved in specific subcomponents of executive functioning, these
6 regions will be differentially activated by each of the tasks. If neural activity in the reorganised
7 auditory cortex can predict behavioural performance in deaf individuals, this will corroborate the
8 functional significance of such plasticity effect.^{20,21}

9 **Materials and Methods**

10 **Participants**

11 There were two groups of participants (see demographics in Supplementary Tables 1-2):

12 a) 29 congenitally or early (before 3 years of age) severely-to-profoundly deaf individuals
13 whose first language is British Sign Language (BSL) and/or English (Supplementary
14 Table 3). We recruited a larger number of deaf participants to reflect the language
15 variability of the deaf population in the UK, as discussed in the “Language assessment”
16 section. Datasets from three deaf participants were excluded from all analyses due to
17 excessive motion in the scanner. One participant was excluded because they only had a
18 mild hearing loss in their best ear (pure-tone average (PTA) less than 25dB). In total, 25
19 deaf participants were included in the analysis of at least one executive function task (see
20 Supplementary Table 4 for details on exclusion).

21 b) 20 hearing individuals who are native speakers of English with no knowledge of any
22 sign language.

23 Deaf and hearing participants were matched on age, gender, nonverbal intelligence, and
24 visuospatial working memory span (Supplementary Table 2).

25 All participants gave written informed consent. All procedures followed the standards set by the
26 Declaration of Helsinki and were approved by the ethics committee of the School of Psychology

1 at the University of East Anglia (UEA) and the Norfolk and Norwich University Hospital
2 (NNUH) Research and Development department.

3 Participants were recruited through public events, social media, and participant databases of the
4 UCL (University College London) Deafness, Cognition and Language Research Centre (DCAL)
5 and the UEA School of Psychology. Participants were all right-handed (self-reported), had full or
6 corrected vision, and no history of neurological conditions. All participants were compensated
7 for their time, travel, and accommodation expenses.

8 **General procedure**

9 Participants took part in one behavioural and one scanning session. The sessions took place on
10 the same or different days.

11 The behavioural session included:

12 a) *Standardised nonverbal IQ and working memory tests*: the Block Design subtest
13 of the Wechsler Abbreviated Scale of Intelligence²² (WASI) and the Corsi Block-tapping
14 test²³ implemented in PEBL software²⁴ (<http://pebl.sourceforge.net/>).

15 b) *Language tasks*: four tasks were administered to assess language proficiency in
16 English and BSL in deaf participants (see the “Language assessment” section below).

17 c) *Pre-scanning training*: the training session ensured that participants understood
18 the tasks and reached accuracy of at least 75%. The tasks were explained in the
19 participant’s preferred language (English or BSL). A written description of all the tasks
20 was provided to all participants (deaf and hearing) to support the experimenter’s
21 explanation.

22 d) *Audiogram screening*: pure-tone averages (PTAs) were used to measure the
23 degree of deafness in deaf participants. Copies of audiograms were provided by the
24 participants from their audiology clinics or were collected at the time of testing using a

1 Resonance R17 screening portable audiometer. Participants included in the study had a
2 mean PTA greater than 75dB averaged across the speech frequency range (0.5, 1, 2kHz)
3 in both ears (mean=93.66±7.79dB; range: 78.33-102.5dB). Four participants did not
4 provide their audiograms, but they were all congenitally severely or profoundly deaf and
5 communicated with the researchers using BSL or relying on lipreading.

6 During the scanning session, fMRI data were acquired while participants performed four visual
7 executive function tasks on switching, working memory, planning, and inhibition (see details
8 below). The order of the tasks was counterbalanced across participants.

9 **Experimental design**

10 All tasks were designed so that each had one condition with higher executive demands (Higher
11 Executive Function; HEF) and one with lower demands (Lower Executive Function; LEF)
12 (Figure 1).

13 *Switching.* In this task, participants had to respond to the shape of geometric objects, i.e., a
14 rectangle and a triangle^{29,30} (Figure 1). At the beginning of the run, participants were instructed
15 to press a key with their left hand when they saw a rectangle and with their right hand when they
16 saw a triangle. Each block started with a cue indicating that the task was to either keep the rule
17 they used in the previous block (“stay” trials; LEF) or to switch it (“switch” trials; HEF). In the
18 switch trials, participants had to apply the opposite mapping between the shape and the response
19 hand. Each block included the presentation of the instruction cue (200ms), a fixation cross
20 (500ms), and two to five task trials. During each trial, a geometrical shape (either a blue
21 rectangle or a blue triangle) was shown at the centre of the screen until the participant responded
22 for a max of 1500ms. Visual feedback (500ms) followed the participant’s response. There were
23 230 trials in 80 blocks of either the LEF (40) or HEF (40) condition. The analysis for the HEF
24 condition only included the first trial of the switch block (see below).

25 *Working memory.* We used a visuospatial working memory task^{25,26} (Figure 1) contrasted with a
26 perceptual control task. A visual cue (1500ms) indicated which task participants should perform.

1 The cue was followed by a 3x4 grid. Black squares were displayed two at a time at random
2 locations on the grid, three times, for a total of 1000ms. In the HEF condition, participants were
3 asked to memorise the six locations. Then they indicated their cumulative memory for these
4 locations by choosing between two grids in a two-alternative, forced-choice paradigm via a
5 button press. The response grids were displayed until the participant responded or for a
6 maximum of 3750ms. In the control condition (LEF), participants indicated whether a blue
7 square was present in any of the grids, ignoring the configuration of the highlighted squares.
8 Trials were separated by an inter-trial interval (ITI) with duration jittered between 2000-3500ms.
9 Each experimental run had 30 working memory trials and 30 control trials.

10 *Planning.* We used a computer version of the classic Tower of London task^{27,28} (Figure 1). In
11 each trial, two configurations of coloured beads placed on three vertical rods appeared on a grey
12 screen, with the tallest rod containing up to three beads, the middle rod containing up to two
13 beads, and the shortest rod containing up to one bead. In the Tower of London condition (HEF),
14 participants had to determine the minimum number of moves needed to transform the starting
15 configuration into the goal configuration following two rules: 1) only one bead can be moved at
16 a time; 2) a bead cannot be moved when another bead is on top. There were four levels of
17 complexity, depending on the number of moves required (2, 3, 4, and 5). In the control condition
18 (LEF), participants were asked to count the number of yellow and blue beads in both displays.
19 For both conditions, two numbers were displayed at the bottom of the screen: one was the correct
20 response and the other was incorrect by +1 or -1. Participants answered with their left hand when
21 they chose the number on the left side of the screen, and with their right hand when their choice
22 was on the right. The maximum display time for each stimulus was 30 seconds. The duration of
23 the ITI was jittered between 2000-3500ms. There were 30 trials in the Tower of London
24 condition and 30 trials in the control condition.

25 *Inhibition.* To study inhibitory control, we used Kelly and Milham's version of the classic Simon
26 task (<https://exhibits.stanford.edu/data/catalog/zs514nn4996>).³¹ A square appeared on the left or
27 the right side of the fixation cross. The colour of the squares was the relevant aspect of the
28 stimuli, with their position irrelevant for the task. Participants were instructed to respond to the
29 red square with the left hand and the green square with the right hand. In the congruent condition

1 (LEF), the button press response was spatially congruent with the location of the stimuli (e.g. the
2 right-hand response for a square appearing on the right side of the screen) (Figure 1). In the
3 incongruent condition (HEF), the correct answer was in the opposite location in respect to the
4 stimulus. Half of the trials were congruent, and half were incongruent. Each stimulus was
5 displayed for 700ms, with a response window of up to 1500ms. The ITI was 2500ms for most
6 trials, with additional blank intervals of 7.5 seconds (20), 12.5 seconds (2), and 30 seconds (1).
7 Participants completed 1 or 2 runs of this task, each consisting of a maximum of 200 trials.

8 **Statistical analysis of behavioural performance**

9 Averaged accuracy (%correct) and reaction time (RT) were calculated. For each participants' set
10 of RTs, we excluded outlier values where participants responded too quickly or where they took
11 a long time to respond. We did this by calculating each participant's interquartile range
12 separately, and then removing values that were more than 1.5 interquartile ranges below the first
13 quartile or above the third quartile of the data series. Differences between groups on accuracy or
14 RT were investigated with repeated-measures ANOVAs with between-subjects factor group
15 (hearing, deaf) and within-subjects factor condition (LEF, HEF).

16 In the switching task, the accuracy switch cost ($\text{SwitchCost}_{\text{ACC}}$) was calculated as the difference
17 in the percent of errors (%errors) between the first switch trial of a switch block and all stay
18 trials. RT switch cost ($\text{SwitchCost}_{\text{RT}}$) was calculated as the difference in RT between the first
19 switch trial of a switch block and all stay trials.

20 In the inhibition task, the Simon effect was calculated as the difference in %errors or RT
21 between the incongruent and congruent trials.

22 **Image acquisition**

23 Images were acquired at the Norfolk and Norwich University Hospital (NNUH) in Norwich, UK,
24 using a 3 Tesla wide bore GE 750W MRI scanner and a 64-channel head coil. Communication
25 with the deaf participants occurred in BSL through a close-circuit camera, or through written
26 English through the screen. An intercom was used for communication with hearing participants.
27 All volunteers were given ear protectors. Stimuli were presented with PsychoPy software³²
28 (<https://psychopy.org>) through a laptop (MacBook Pro, Retina, 15-inch, Mid 2015). All stimuli

1 were projected by an AVOTEC's Silent Vision projector ([https://www.avotecinc.com/high-](https://www.avotecinc.com/high-resolution-projector)
2 [resolution-projector](https://www.avotecinc.com/high-resolution-projector)) onto a screen located at the back of the magnet's bore. Participants watched
3 the screen through a mirror mounted on the head coil. Button responses were recorded via fORP
4 (Fiber Optic Response Pads) button boxes ([https://www.crsLtd.com/tools-for-functional-](https://www.crsLtd.com/tools-for-functional-imaging/mr-safe-response-devices/forp/)
5 [imaging/mr-safe-response-devices/forp/](https://www.crsLtd.com/tools-for-functional-imaging/mr-safe-response-devices/forp/)). Functional imaging data were acquired using a
6 gradient-recalled echo (GRE) EPI sequence (50 slices, TR=3,000ms, TE=50ms,
7 FOV=192x192mm, 2mm slice thickness, distance factor 50%) with an in-plane resolution of
8 3x3mm. The protocol included six functional scans: five task-based fMRI scans (switching: 10.5
9 minutes, 210 volumes; working memory: 11 minutes, 220 volumes; planning: 11.5 minutes, 230
10 volumes; inhibition: two runs of 10 minutes, 200 volumes each) and one resting state scan (part
11 of a different project, and to be reported in a different manuscript). Some participants did not
12 complete all functional scans (Supplementary Table 4). An anatomical T1-weighted scan (IR-
13 FSPGR, TI=400ms, 1mm slice thickness) with an in-plane resolution of 1x1mm was acquired
14 during the session.

15 Raw B0 field map data were acquired using a 2D multi-echo GRE sequence with the following
16 parameters: TR=700ms, TE=4.4 and 6.9ms, flip angle=50°, matrix size=128x128,
17 FOV=240mmx240mm, number of slices=59, thickness=2.5mm, and gap=2.5mm. Real and
18 imaginary images were reconstructed for each TE to permit calculation of B0 field maps in
19 Hz.³³⁻³⁵

20 **fMRI preprocessing**

21 fMRI data were analysed with MATLAB 2018a (MathWorks, MA, USA) and Statistical
22 Parametric Mapping software (SPM12; Wellcome Trust Centre for Neuroimaging, London,
23 UK).³⁶ The anatomical scans were segmented into different tissue classes: grey matter, white
24 matter, and cerebrospinal fluid. Skull-stripped anatomical images were created by combining the
25 segmented images using the Image Calculation function in SPM (ImCalc,
26 <http://tools.robjellis.net>). The expression used was: $[(i1.*(i2+i3+i4))>threshold]$, where $i1$ was
27 the bias-corrected anatomical scan and $i2$, $i3$ and $i4$ were the tissue images (grey matter, white
28 matter, and cerebrospinal fluid, respectively). The threshold was adjusted between 0.5 and 0.9 to
29 achieve adequate brain extraction for each participant. Each participant's skull-stripped image

1 was normalised to the standard MNI space (Montreal Neurological Institute) and the deformation
2 field obtained during this step was used for normalisation of the functional scans. Susceptibility
3 distortions in the EPI images were estimated using a field map that was co-registered to the
4 BOLD reference.^{33,34} Images were realigned using the pre-calculated phase map, co-registered,
5 slice-time corrected, normalised, and smoothed (using an 8mm FWHM Gaussian kernel). All
6 functional scans were checked for motion and artefacts using the ART toolbox
7 (https://www.nitrc.org/projects/artifact_detect).

8 **fMRI first-level analysis**

9 The first-level analysis was conducted by fitting a general linear model (GLM) with regressors of
10 interest for each task (see details below). All the events were modelled as a boxcar and
11 convolved with SPM's canonical hemodynamic response function. The motion parameters,
12 derived from the realignment of the images, were added as regressors of no interest. Regressors
13 were entered into a multiple regression analysis to generate parameter estimates for each
14 regressor at every voxel.

15 *Switching.* The first trial of each switch block (HEF) and all stay trials (LEF) were modelled as
16 regressors of interest separately for the left- and right-hand responses. The cues and the
17 remaining switch trials were included as regressors of no interest.

18 *Working memory.* The conditions of interest were working memory (HEF) and control (LEF).
19 The onset was set at the presentation of the first grid, with the duration set at 3.5 seconds (i.e.,
20 the duration of the three grids plus a 500ms blank screen before the appearance of the response
21 screen; Figure 1). Button responses were included separately for each hand and condition as
22 regressors of no interest.

23 *Planning.* Tower of London (HEF) and control (LEF) conditions were included in the model as
24 regressors of interest, with onsets at the beginning of each trial and duration set to the trial-
25 specific RT. Button responses were modelled separately for each hand as regressors of no
26 interest.

1 *Inhibition.* Four regressors of interest were obtained by combining the visual hemifield where the
2 stimulus appeared with the response hand (1. right visual hemifield—left hand; 2. left visual
3 hemifield—right hand; 3. right visual hemifield—right hand; 4. left visual hemifield—left hand).
4 Right visual hemifield—left hand and left visual hemifield—right hand were the incongruent
5 conditions (HEF), whereas the right visual hemifield-right hand and left visual hemifield-left
6 hand were the congruent conditions (LEF).

7 **Region of interest analysis**

8 We conducted a region of interest (ROI) analysis to investigate crossmodal plasticity and
9 differences between groups in the auditory cortex. Three auditory regions of the superior
10 temporal cortex were included in this analysis: Heschl's gyrus (HG), the planum temporale (PT),
11 and the posterior superior temporal cortex (pSTC) (Figure 2). HG and the PT were defined
12 anatomically, using FreeSurfer software³⁷ (<https://surfer.mmr.mgh.harvard.edu>). Full descriptions
13 of these procedures can be found elsewhere^{38,39}, but in short, each participant's bias-corrected
14 anatomical scan was parcellated and segmented, and voxels with the HG label and the PT label
15 were exported using SPM's ImCalc function
16 (http://robjellis.net/tools/imcalc_documentation.pdf). Participant-specific ROIs were then
17 normalised to the standard MNI space using the deformation field from the normalisation step of
18 the preprocessing.

19 pSTC was specified following findings from Cardin et al.'s study⁴, where a visual working
20 memory crossmodal plasticity effect was found in right and left pSTC in deaf individuals [left: -
21 59 -37 10; right: 56 -28 -1]. Right and left functional pSTC ROIs were defined using data from
22 Cardin et al.³, with the contrast [deaf (working memory > control task) > hearing (working
23 memory > control task)] ($p < 0.005$, uncorrected).

24 There was an average partial overlap of 8.2 voxels ($SD = 6.86$) between left PT and left pSTC,
25 with no significant difference in overlap between groups (deaf: mean=9.92, $SD = 7.02$; hearing:
26 mean=6.05, $SD = 6.17$). To ensure that the two ROIs were independent, common voxels were
27 removed from left PT in a subject-specific manner. Removing the overlapping voxels did not
28 qualitatively change the results.

1 Parameter estimates for each participant were extracted from each ROI using MarsBaR 0.44⁴⁰
2 (<http://marsbar.sourceforge.net>). The data were analysed using JASP⁴¹ (<https://jasp-stats.org>) and
3 entered into separate repeated-mixed measures ANOVAs for each task and set of ROIs. Factors
4 in the ANOVAs on the temporal ROIs included: the between-subjects factor group (hearing,
5 deaf) and the within-subjects factors ROI (HG, PT, pSTC), hemisphere (left, right), and
6 condition (LEF, HEF).
7 The Greenhouse-Geisser correction was applied when the assumption of sphericity was violated.
8 Significant interactions and effects of interest were explored with Student's t-tests or Mann-
9 Whitney U-tests when the equal variance assumption was violated.

10 **Language assessment**

11 We recruited a representative group of the British deaf population, who usually have different
12 levels of proficiency in sign and spoken language. This was: 1) to study plasticity in a
13 representative group of deaf individuals; 2) to study the relationship between language
14 experience and the organisation of cognitive networks of the brain, which will be reported in a
15 separate manuscript.

16 To assess the language proficiency of deaf participants, we chose grammaticality judgement tests
17 measuring language skills in English and BSL. The BSL grammaticality judgement task
18 (BSLGJT) is described in Cormier et al.'s paper⁴², and the English grammaticality judgement
19 task (EGJT) was designed based on examples from Linebarger et al.'s paper⁴³. The BSLGJT and
20 the EGJT use a single method of assessing grammaticality judgements of different syntactic
21 structures in English and BSL. Grammaticality judgement tests have been used in deaf
22 participants before and have proved to be efficient in detecting differences in language
23 proficiency among participants with varying ages of acquisition.^{42,44} Deaf participants performed
24 both the BSL and English tests if they knew both languages, or only the English tests if they did
25 not know BSL.

26 To control for potential language proficiency effects, we combined results from the English and
27 BSL grammaticality judgement tasks (EGJT and BSLGJT) to create a single, modality-
28 independent measure of language proficiency in the deaf group. Accuracy scores in the EGJT

1 (%correct; mean=83.51, SD=11.4, N=25) and BSLGJT (mean=77.88, SD=13.1, N=21) were
2 transformed into z-scores separately for each test. For each participant, the EGJT and BSLGJT z-
3 scores were then compared, and the higher one was chosen for a combined modality-independent
4 language proficiency score (Supplementary Figure 1).

5 **Multiple linear regression**

6 Multiple linear regression analyses were conducted to investigate whether neural activity in the
7 superior temporal cortex of deaf individuals can predict performance in the switching task. The
8 data were analysed using a backward data entry method in JASP.⁴¹ The default stepping method
9 criteria were used, where predictors with $p < .05$ are entered into the model and those with $p >$
10 0.1 are removed until all predictors fall within these criteria. SwitchCost_{RT} and SwitchCost_{ACC}
11 were entered as dependent variables in separate analyses. Each regression analysis had three
12 covariates: neural switch cost in the right hemisphere, neural switch cost in the left hemisphere,
13 and language.

14 Neural switch cost ($BOLD_{\text{switch}} - BOLD_{\text{stay}}$) was calculated in ROIs with significant differences
15 between the switch and stay condition in the deaf group. The average neural activity in all stay
16 trials ($BOLD_{\text{stay}}$) was subtracted from the average activity in the first switch trials ($BOLD_{\text{switch}}$),
17 and then averaged across ROIs separately in the right and left hemisphere.

18 **Data availability**

19 Link to data and analysis files: <https://osf.io/uh2ap/>

20 **Results**

21 **Behavioural results**

22 Deaf (N=25) and hearing (N=20) individuals were scanned while performing four executive
23 function tasks: switching, working memory, planning, and inhibition (Figure 1). Behavioural
24 results from all tasks are shown in Figure 3. To explore differences in performance between

1 groups, we conducted 2x2 repeated-measures ANOVAs for each task, with either accuracy or
2 reaction time (RT) as the dependent variable, between-subjects factor group (hearing, deaf), and
3 within-subjects factor condition (HEF, LEF). Results show a significant main effect of condition
4 for both accuracy and RT in all tasks, confirming that the HEF condition was more difficult and
5 demanding than the LEF condition (Supplementary Table 5).

6 The group of deaf individuals had significantly slower RTs in all tasks (Supplementary Table 5).
7 Switching was the only task where there was a significant main effect of group on accuracy
8 ($F_{1,41}=4.32$, $p=0.04$, $\eta^2_p=0.09$), as well as a condition \times group interaction ($F_{1,41}=4.98$, $p=0.03$,
9 $\eta^2_p=0.11$). A post-hoc t-test revealed a significant between-groups difference, where the group of
10 deaf individuals was significantly less accurate than the group of hearing individuals in the
11 switch condition ($t_{41}=-2.22$, $p=0.03$, $d=0.68$). The difference in $\text{SwitchCost}_{\text{ACC}}$ ($\% \text{error}_{\text{Switch}} -$
12 $\% \text{error}_{\text{Stay}}$) reflects the significant interaction, with the deaf group (mean=10.24, $SD=9.89$,
13 $t_{22}=4.96$, $p<0.001$, $d=1.03$) having a larger $\text{SwitchCost}_{\text{ACC}}$ than the hearing group (mean=4.18;
14 $SD=7.53$, $t_{19}=2.49$, $p=0.02$, $d=0.56$; Figure 3B).

15 **fMRI Results**

16 fMRI results show that all executive function tasks activated typical frontoparietal regions in
17 both groups of participants (Supplementary Figure 2). There were significantly stronger
18 activations in the HEF condition in the switching, working memory, and planning tasks. These
19 included commonly found activations in frontoparietal areas, such as dorsolateral prefrontal
20 cortex (DLPFC), frontal eye fields (FEF), pre-supplementary motor area (pre-SMA), and
21 intraparietal sulcus (IPS). In the inhibition task, the HEF incongruent condition resulted in
22 stronger activation in IPS and left FEF, but there were no significant differences between
23 conditions.

24 To investigate crossmodal plasticity and executive processing in the auditory cortex of deaf
25 individuals, we conducted a region of interest (ROI) analysis on superior temporal auditory
26 ROIs. These included: Heschl's gyrus (HG), the planum temporale (PT), and the posterior
27 superior temporal cortex (pSTC) (Figure 2). Differences and interactions between groups are
28 discussed below, and we first present results from the switching task, where we observed the

1 strongest activations of temporal ROIs in the deaf group (Figure 4). Results from all other tasks
2 are discussed in the following sub-section.

3 **Task switching activates auditory areas in deaf individuals and this activation predicts** 4 **behaviour**

5 Of the four tasks that we tested, only in the switching task we found both a significant main
6 effect of group ($F_{1,41}=15.48$, $p<0.001$, $\eta^2_p=0.27$) and a significant interaction between group x
7 condition ($F_{1,41}=4.75$, $p=0.03$, $\eta^2_p=0.10$) (Table 1). The interaction was driven by a significant
8 difference between conditions in the deaf group, but not in the hearing group (deaf_{HEFvLEF}:
9 $t_{22}=4.06$, $p<0.001$, $d=0.85$; hearing_{HEFvLEF}: $t_{19}=0.26$, $p=0.79$, $d=0.06$). To test whether
10 differences between conditions were significant between the switch and stay condition in all
11 ROIs, we conducted post-hoc t-tests in each ROI and group. This accounted for a total of 12
12 separate t-tests, and to correct for multiple comparisons, we only considered significant those
13 results with $p < 0.004$ ($p < 0.05/12 = 0.004$; corrected $p < 0.05$). We found significant differences
14 between the switch and stay condition in all the left hemisphere ROIs and in the right PT and
15 right pSTC in the deaf group (Figure 4; Supp. Table 6).

16 To investigate the behavioural relevance of the observed crossmodal plasticity, we evaluated
17 whether neural activity in the superior temporal cortex of deaf individuals can predict
18 performance during the switching task. We conducted two separate multiple linear regression
19 analyses, one with SwitchCost_{RT} and one with SwitchCost_{ACC} as dependent variables (Table 2).
20 The covariates included in the model were: right hemisphere neural switch cost, left hemisphere
21 neural switch cost, and language z-scores. For the neural switch cost covariates, data was
22 averaged from ROIs in the right and left hemisphere in order to reduce the number of dimensions
23 in the multiple linear regression models. To do this, we calculated the neural switch cost
24 ($BOLD_{switch} - BOLD_{stay}$) for each ROI with significant differences in activity between the switch
25 and stay conditions in the deaf group (Figure 4; Supp. Table 6), and we then averaged neural
26 switch cost separately for ROIs in the right and left hemisphere. We also included language as a
27 covariate in our models because language proficiency has been shown to modulate performance
28 in EF tasks in deaf individuals.⁴⁵⁻⁴⁸

1 Results from the multiple linear regression analysis using backward data entry show that neural
 2 activity in temporal ROIs can significantly predict SwitchCost_{RT} in the deaf group (Table 2). The
 3 most significant model included both right and left hemisphere neural switch cost as covariates,
 4 and explained 40.6% of the variance ($F(2,18)=6.15$, $p=0.009$, $R^2=0.41$, adjusted $R^2=0.34$; Table
 5 2, Top panel). There was a positive association between SwitchCost_{RT} and neural switch cost in
 6 right hemisphere temporal areas ($B=0.04$, $SE=0.01$, $\beta=0.99$; $p=0.003$). This means that for
 7 every unit increase in neural switch cost in right temporal areas, there is an increase of 40ms in
 8 SwitchCost_{RT}. In standardised terms, as neural switch cost increases by 1 standard deviation,
 9 SwitchCost_{RT} increases by 0.99 SDs. On the other hand, there was a negative association
 10 between the left hemisphere neural and SwitchCost_{RT}. However, this was only significant in the
 11 full model ($p=0.031$, $B=-0.02$, $SE=0.01$, $\beta=-0.69$), but not in the best model ($p=0.05$, $B=-0.02$,
 12 $SE=0.01$, $\beta=-0.61$; Table 2). There was no significant association between SwitchCost_{RT} and
 13 language ($B=-0.06$, $SE=0.05$, $\beta=-0.23$; $p=0.22$).

14 When evaluating whether neural switch cost could also predict SwitchCost_{ACC}, we found no
 15 significant association between these variables (Table 2, Bottom panel). Instead, the most
 16 significant model included only language as a regressor (Table 2), explaining 20.7% of the
 17 variance ($F(1,19)=4.96$, $p=0.04$, $R^2=0.21$, adjusted $R^2=0.16$). For every unit increase in language
 18 z-scores, there is a decrease of 12.6 units in SwitchCost_{ACC}. In standardised terms, as language z-
 19 scores increased by 1 standard deviation, SwitchCost_{ACC} decreased by 0.45 SDs.

20 **Recruitment of auditory areas in deaf individuals is not ubiquitous across EF tasks**

21 Results from the working memory, planning and inhibition tasks are shown in Figure 5. In the
 22 working memory task, there was a significant condition \times group interaction (Table 1, $F_{1,41}=6.41$,
 23 $p=0.01$, $\eta^2_p=0.13$), but differences between conditions within each group were not significant
 24 (hearing_{HEFvLEF}: $t_{18}=-1.74$, $p=0.10$, $d=-0.40$; deaf_{HEFvLEF}: $t_{23}=1.81$, $p=0.08$, $d=0.37$). In the
 25 planning task, there was a significant main effect of group ($F_{1,38}=5.85$, $p=0.02$, $\eta^2_p=0.13$), but
 26 this was driven by significant deactivations in the hearing group ($t_{18}=-4.47$, $p<0.001$, $d=-1.00$),
 27 with no significant difference in activity from baseline in the deaf group ($t_{20}=-1.31$, $p=0.21$, $d=-$
 28 0.29). In the Inhibition task, there was a significant interaction between ROI and Group

1 ($F_{1.89,66.05}=3.92$, $p=0.03$, $\eta^2_p=0.10$). However, there were no significant differences between
2 groups in any ROI (<https://osf.io/9fuec>). Instead, the ROI x group interaction was driven by a
3 main effect of ROI in the deaf group (higher activations for PT and pSTC than HG,
4 <https://osf.io/2z35e/>), which was not present in the hearing group (<https://osf.io/gmy6v/>).

5 **Discussion**

6 We investigated how early sensory experience impacts the organisation of executive processing
7 in the brain. We found that, in deaf individuals, primary and secondary auditory areas are
8 recruited during a visual switching task. These results suggest that the sensory or cognitive
9 specialisation of cortical regions in the adult brain can be influenced by developmental sensory
10 experience. It is possible that an early absence of auditory inputs results in a shift of functions in
11 regions typically involved in auditory processing, with these regions then adopting a role in
12 specific components of executive processing. Neural activity in temporal regions during the
13 switching task predicted performance in deaf individuals, highlighting the behavioural relevance
14 of this functional shift.

15 Our design allowed us to thoroughly examine the role of auditory regions in different executive
16 function tasks and determine whether these regions are involved in cognitive control. Previous
17 studies have suggested an involvement of auditory cortex during higher-order cognitive tasks in
18 deaf individuals^{4,5}, but given the focus on a single task, with an experimental and control
19 condition, they cannot inform whether plasticity effects are specific to the demands of the task.
20 Our design included four different visuospatial EF tasks, all with an experimental (HEF) and
21 control (LEF) condition, probing a variety of executive processes. We found that the HEF
22 condition in all tasks recruited frontoparietal areas typically involved in executive functioning
23 and cognitive control. However, only switching resulted in significant activations in temporal
24 auditory regions in the deaf group. This finding demonstrates that the auditory cortex of deaf
25 individuals serves a specific subcomponent of executive functioning during switching, and not a
26 shared computation across tasks, such as cognitive control. This was not only found in higher-
27 order auditory areas, but also in the left Heschl's Gyrus, showing that a functional shift towards
28 cognition can indeed occur in primary sensory regions. A significant activation during the

1 switching condition in the left, but not the right HG, provides further evidence for different roles
2 of left and right temporal regions in deaf individuals (see Cardin et al.⁷ for a review). Differences
3 in the recruitment of the left and right HG in this study may be linked to the specialisation of
4 these regions for sound processing in hearing individuals. In this group, left HG is specialised for
5 the temporal processing of auditory signals, whereas the right HG shows stronger sensitivity to
6 spectral components⁴⁹. The switching task in this study requires tracking a sequence of stimuli in
7 time, whilst the extraction of spectral or frequency information is not needed in this task, which
8 could explain the different recruitment of HG across hemispheres. The fact that right HG was not
9 recruited during the switching task, while right PT and pSTC were, also suggests a functional
10 difference in crossmodal plasticity between primary and secondary auditory regions. Primary
11 auditory regions are the first cortical relay of auditory inputs and have stronger subcortical inputs
12 from the thalamus⁵⁰, while secondary regions might be more likely to be modulated by top-down
13 influences, potentially driving plastic reorganisation in different directions. Further studies
14 focusing on finer-grain mapping of crossmodal plasticity effects in the auditory cortex of deaf
15 individuals are needed in order to elucidate these processes.

16 Task switching requires cognitive flexibility and shifting between different sets of rules.^{51,52}
17 Shifting is considered one of the core components of executive control. It is defined as the ability
18 to flexibly shift “back and forth between multiple tasks, operations, or mental sets”.⁵³ Shifting is
19 also an important component of working memory tasks previously shown to recruit posterior
20 superior temporal regions in deaf individuals (e.g. 2-back working memory, visuospatial delayed
21 recognition^{4,5}). In the present study, the working memory task did not significantly activate any
22 temporal ROI. The working memory task used in this study requires updating of information and
23 incremental storage, but no shifting between targets or internal representations of stimuli, as
24 required in an n-back task. Together, these results suggest that previous working memory effects
25 in superior temporal regions are not necessarily linked to storage, updating or control, but are
26 more likely linked to shifting between tasks or mental states.

27 A change of function in the auditory cortex, specifically in the right hemisphere, could be
28 explained by the anatomical proximity to the middle temporal lobe or to the parietal lobe,
29 specifically the temporoparietal junction (TPJ).^{7,54} Right TPJ is a multisensory associative region

1 involved in reorientation of attention to task-relevant information, such as contextual cues or
2 target stimuli.^{55,56} Regions of the right middle temporal gyrus have also been shown to be
3 involved in task switching⁵⁷ and to encode task-set representations.⁵⁸ In the absence of auditory
4 inputs throughout development, the proximity to the TPJ and the middle temporal gyrus may
5 result in changes in the microcircuitry or in the computations performed by the adjacent auditory
6 cortices, where these regions now perform computations that allow switching between
7 tasks.^{7,54,58} This is particularly relevant for the right hemisphere, where activity in auditory
8 regions was more strongly linked to behavioural outcomes in the switching task in the group of
9 deaf individuals.

10 Another possibility is that the recruitment of “auditory” temporal regions for switching observed
11 in deaf adults reflects vestigial functional organisation present in early stages of development.
12 Research on hearing children has found activations in bilateral occipital and superior temporal
13 cortices during task switching⁶⁰, with a similar anatomical distribution to the one we find here.
14 Our findings in deaf individuals suggest that executive processing in temporal cortices could be
15 “displaced” by persistent auditory inputs which, as the individual develops, may require more
16 refined processing or demanding computations. Thus, an alternative view is that regions
17 considered to be “sensory” have mixed functions in infants and become more specialised in
18 adults. These regions could follow different developmental pathways influenced by
19 environmental sensory experience. As such, the temporal regions of hearing individuals will
20 become progressively more specialised for sound processing, whereas, in deaf individuals, they
21 will become more specialised for subcomponents of executive processing.

22 The direct relationship between behavioural outcomes and activity in reorganised cortical areas
23 is robust evidence of the functional importance of the observed crossmodal plasticity. We found
24 that neural activity, specifically in the right temporal ROIs, predicted reaction times in the
25 switching task in the deaf group. Specifically, higher neural switch cost was linked to higher RT
26 switch cost ($\text{SwitchCost}_{\text{RT}}$), which suggests effortful processing, as previously described in other
27 cognitive tasks with different levels of complexity.^{61,62} It is important to highlight that there were
28 no differences in $\text{SwitchCost}_{\text{RT}}$ between the groups, showing that the potential reliance on
29 different neural substrates to solve the switching task does not translate into differences in

1 performance. In fact, significant interactions between group and condition for the switching task
2 were only found in accuracy (SwitchCost_{ACC}), which in our analysis was not predicted by neural
3 activity, but rather, by language proficiency. Executive performance has been previously
4 associated with language proficiency in deaf children.^{47,48,63–65} While in our study language z-
5 scores predict only 20.7% of the variance in SwitchCost_{ACC} and the model was only significant at
6 $p < 0.05$, our findings suggest that language development can have long-lasting effects on
7 executive processing throughout the lifespan. Different theories propose that language can
8 provide the necessary framework for higher-order (if-if-then) rules to develop and be used in a
9 dynamic task in the most efficient way.^{66,67} These hierarchical “if-then” rules could be
10 implemented, in an automatic way, to solve the arbitrary link between stimulus and response
11 during switching. Although participants are not required to use linguistic strategies during
12 switching, we speculate that those who have benefited from the efficiency associated with
13 developing such frameworks can invest less cognitive resources into solving this task. While the
14 role of language in executive processing needs further investigation, it is important to consider
15 that the timely development of a first language may boost the overall efficiency of a cognitive
16 task, in this case switching, regardless of whether the task itself allows implementation of purely
17 linguistic mechanisms.

18 It is important to take into account that all signers of BSL are bilingual to a greater or lesser
19 degree, depending on their early language background, degrees of deafness, and educational
20 experiences.⁶⁸ Bilinguals who frequently change languages have generally been shown to have
21 an advantage in executive function switching tasks.^{69–71} However, it is unlikely that differences in
22 bilingualism can explain our findings in this study. If different results between deaf and hearing
23 participants were due to the presence or not of bilingualism, we would have expected the group
24 of deaf individuals to have a behavioural advantage in the switching task, but that was the
25 opposite of what we found. In addition, we have previously shown that working memory
26 responses in the superior temporal cortex of deaf individuals cannot be explained by
27 bilingualism³. In our previous study⁴, we compared deaf native signers to two groups of hearing
28 individuals: 1) hearing native signers, who were bilingual in English and BSL (bimodal
29 bilinguals), and 2) hearing non-signers who were bilingual in English and another spoken
30 language (unimodal bilinguals). These three populations were comparably proficient in both their

1 languages. We found differences in the recruitment of superior temporal regions between deaf
2 individuals and both groups of hearing participants during a working memory task, suggesting a
3 crossmodal plasticity effect driven by different sensory experience⁴. These effects in the superior
4 temporal cortex could not be explained by bilingualism, because this was controlled across
5 groups. In the present study, significant activations during the switching condition were found in
6 the same areas where we previously found working memory activations in deaf individuals (left
7 and right pSTC, which were defined functionally based on our previous findings; see Methods),
8 suggesting that these regions are involved in specific subcomponents of executive processing as
9 a consequence of early deafness.

10 In addition, as a group, deaf participants had significantly longer reaction times in all tasks. This
11 is at odds with behavioural results from studies of deaf native signers, where the performance of
12 this group in executive function tasks is comparable to or faster than that of typically hearing
13 individuals (e.g. Hauser et al.⁴⁶; Marshall et al.⁴⁸; Cardin et al.⁴). Native signers achieve
14 language development milestones at the same rate as that of hearing individuals learning a
15 spoken language, highlighting again the importance of early language access, not only for
16 communication but also for executive processing. Deaf individuals also have faster RTs in
17 studies of visual reactivity,^{21,72} suggesting critical differences in performance between purely
18 perceptual tasks, and those which weigh more strongly on executive demands, where language
19 experience and early language acquisition could have a longer-lasting effect throughout the
20 lifespan.

21 In conclusion, we show that components of executive processing, such as switching, can be
22 influenced by early sensory experience. Our results suggest that, in the absence of auditory
23 inputs, superior temporal regions can take on functions other than sensory processing. This could
24 be either by preserving a function these areas performed early in childhood or by taking on new
25 functions driven by influences from top-down projections from frontoparietal areas or adjacent
26 temporal and parietal regions.

27

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8 **Competing interests**

9 The authors report no competing interests.

10 **Supplementary material**

11 Supplementary material is available at *Brain* online.

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1 **Figure Legends**

2 **Figure 1 Executive function tasks.** Each task had a higher executive demands condition
 3 (HEF=Higher Executive Function, purple) and a lower executive demands condition
 4 (LEF=Lower Executive Function, peach). See Methods for details of the design.

5 **Figure 2 Temporal ROIs analysis summary. A.** Temporal regions included in the analysis:
 6 Heschl's gyrus (HG), the planum temporale (PT), and the superior temporal cortex (pSTC). HG
 7 and PT were defined anatomically, in a subject-specific manner, using the FreeSurfer software
 8 package.³⁶ The figure shows the overlap of all subject-specific ROIs. Common voxels between
 9 left PT and left pSTC have been subtracted from left PT (see Methods). pSTC was defined
 10 functionally, based on the findings of Cardin et al.'s study³ (see Methods).

11 **Figure 3 Behavioural performance.** The figure shows average accuracy (%correct) and
 12 reaction time (seconds) for each task and condition in the hearing and the deaf groups. It also
 13 shows the average switch costs and Simon effects for both accuracy and reaction time in each
 14 group. The SwitchCost_{ACC} and Simon effect are calculated and plotted using %error instead of
 15 %correct, so that larger values indicate an increase in cost. Only the first trials of the switch
 16 blocks were included in the HEF condition. The bold lines in the box plots indicate the median.
 17 The lower and upper hinges correspond to the first and third quartiles. Statistically significant
 18 ($p < 0.05$) differences between conditions are not shown in the figure, but were found for all tasks
 19 in both groups (Suppl. Table 5). ** $p < 0.01$; * $p < 0.05$.

20 **Figure 4 Switching task analysis. A.** Neural activity in temporal ROIs. *** $p < 0.005$;
 21 **** $p < 0.001$. **B.** Partial correlation plot between SwitchCost_{RT} and neural switch cost in right
 22 temporal ROIs in the group of deaf individuals. Partial correlation from a multiple linear model
 23 with SwitchCost_{RT} as dependent variable and the following covariates: right hemisphere neural
 24 switch cost, left hemisphere

25 **Figure 5 ROI results from the working memory, planning and inhibition tasks.** Ctr=control,
 26 WM=working memory, ToL=Tower of London, Con=congruent, Inc=incongruent.
 27 HG=Heschl's gyrus, PT=planum temporale, pSTC=posterior superior temporal cortex.

1 **Table 1 Group main effects and Group interactions for all tasks in the ROIs analysis**

	Switching		Working Memory		Planning		Inhibition	
	F (df)	p	F (df)	p	F (df)	p	F (df)	p
Group	15.48 (1,41)	<0.001	0.04 (1,41)	0.85	5.85 (1,38)	0.02	0.03 (1,35)	0.87
Condition × Group	4.75 (1,41)	0.03	6.40 (1,41)	0.01	0.56 (1,38)	0.46	0.18 (1,35)	0.67
ROI × Group	3.42 (1.9,79.1)	0.04	1.18 (1.7,68.4)	0.30	0.73 (1.7,64.6)	0.46	3.92 (1.9,66.1)	0.03
Hemisphere × Group	0.009 (1,41)	0.92	0.01 (1,41)	0.93	0.46 (1,38)	0.50	0.30 (1,35)	0.59

2 Significant results are indicated in bold. Full results for each ANOVA can be found in OSF: <https://osf.io/dt827/>

5 **Table 2 Multiple Linear Regression predicting behavioural performance in the switching task**

SwitchCost _{RT}						
Model Summary						
Model	R ²	Adjusted R ²	F	p		
1	0.46	0.36	4.78	0.01		
2	0.41	0.34	6.15	0.009		
Coefficients						
Model		Unstandardized	SE	Standardized	t	p
1	(Intercept)	0.025	0.040		0.63	0.53
	Language Score	-0.061	0.048	-0.23	-1.27	0.22
	LH Neural Switch Cost	-0.024	0.010	-0.69	-2.35	0.03
2	(Intercept)	-0.013	0.026		-0.51	0.62
	LH Neural Switch Cost	-0.021	0.010	-0.61	-2.09	0.05
	RH Neural Switch Cost	0.040	0.012	0.99	3.39	0.003
SwitchCost _{ACC}						
Model Summary						
Model	R ²	Adjusted R ²	F	p		
1	0.28	0.16	2.26	0.12		
2	0.28	0.20	3.55	0.05		
3	0.21	0.16	4.96	0.04		
Coefficients						
Model		Unstandardized	SE	Standardized	t	p
1	(Intercept)	15.84	4.82		3.28	0.004
	Language Score	-12.85	5.83	-0.46	-2.20	0.04
	LH Neural Switch Cost	-0.28	1.25	-0.08	-0.22	0.82
2	(Intercept)	15.78	4.69		3.37	0.003
	Language Score	-12.57	5.55	-0.45	-2.27	0.04
	RH Neural Switch Cost	1.41	1.41	0.33	1.00	0.33
3	(Intercept)	18.90	4.20		4.50	<0.001
	Language Score	-12.64	5.68	-0.45	-2.23	0.04

6 Significant results are indicated in bold. LH = left hemisphere; RH = right hemisphere; SE = standard error.

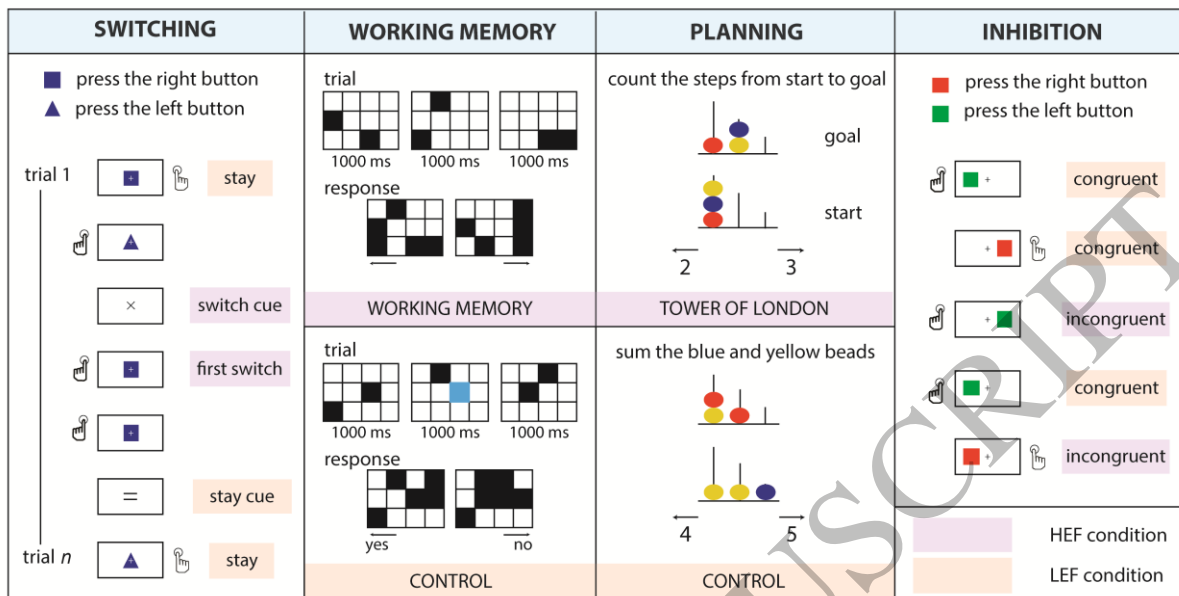


Figure 1
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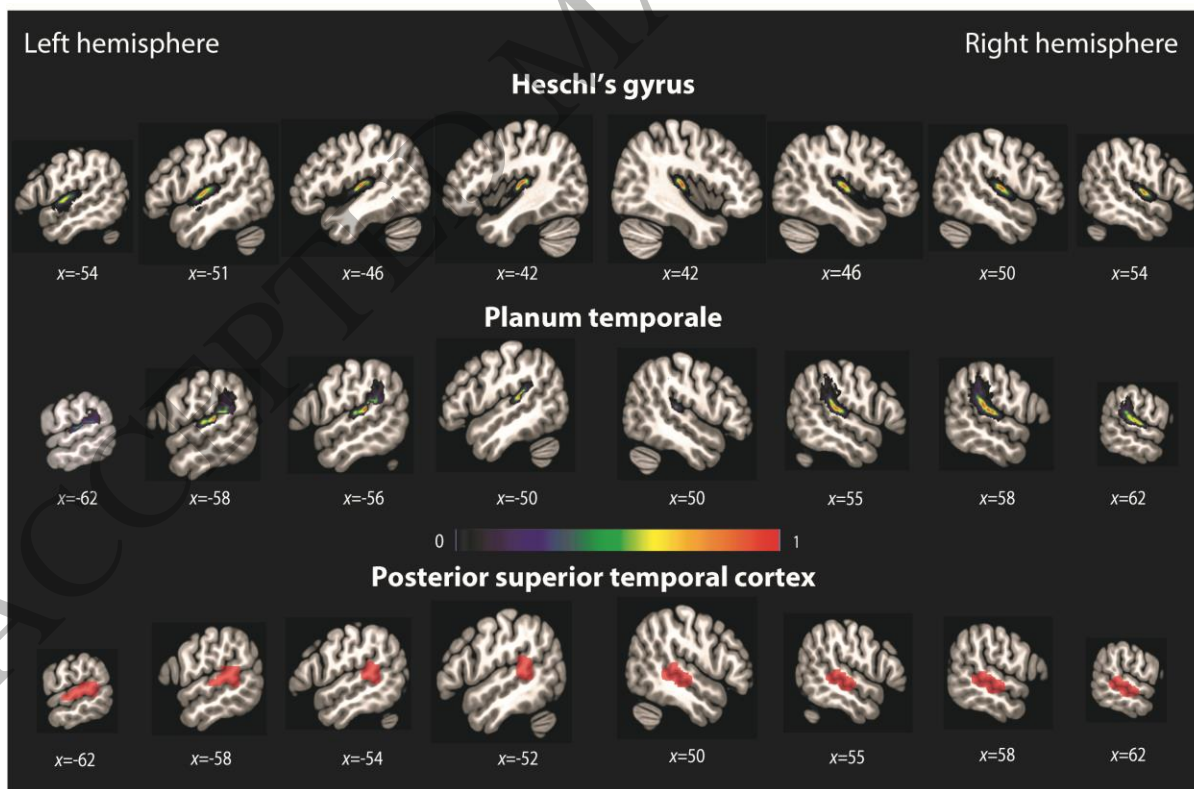


Figure 2
159x105 mm (.74 x DPI)

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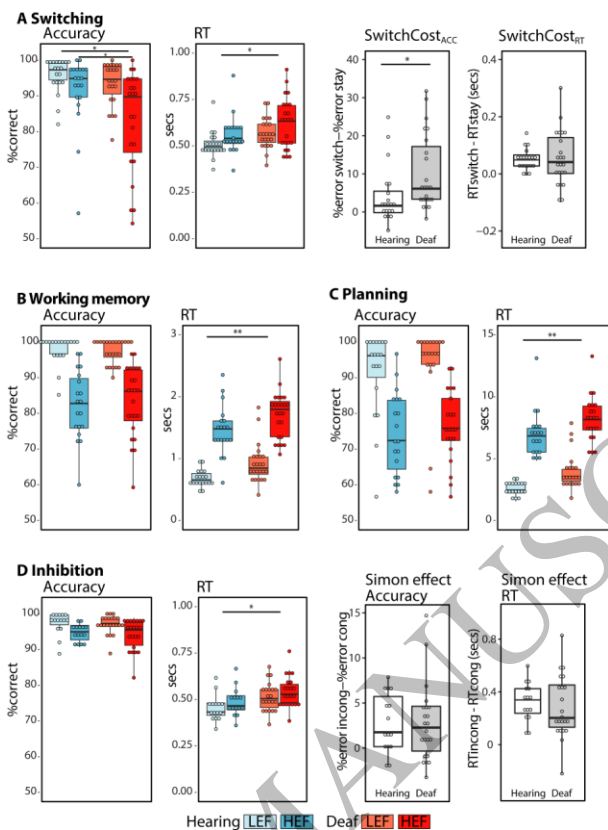


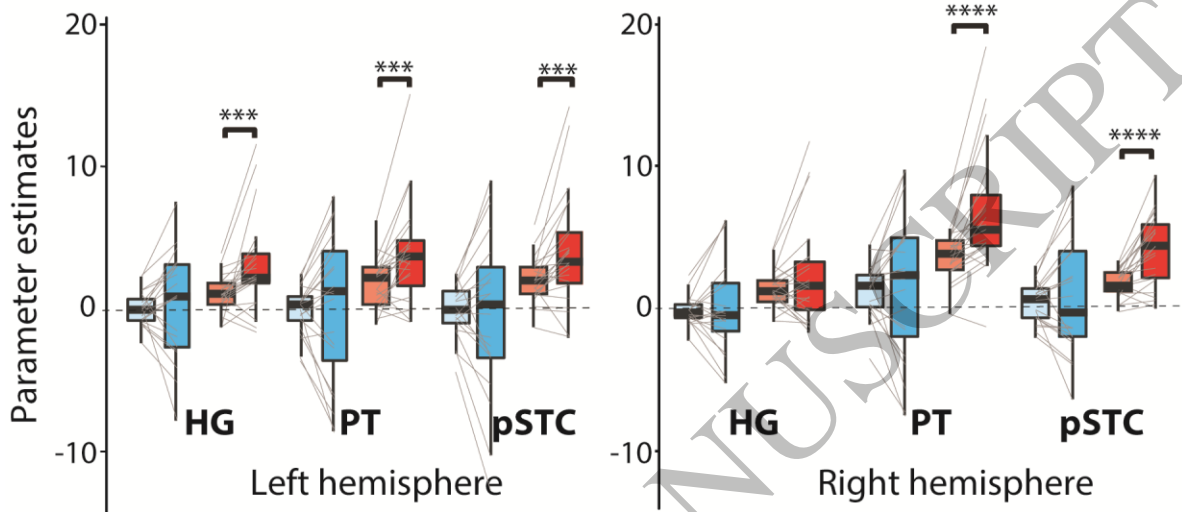
Figure 3
80x108 mm (.74 x DPI)

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Switching

A Neural activity in the temporal regions

Hearing Stay Switch Deaf Stay Switch



B Relationship between neural switch cost and $\text{SwitchCost}_{\text{RT}}$ in right temporal ROIs in the deaf group

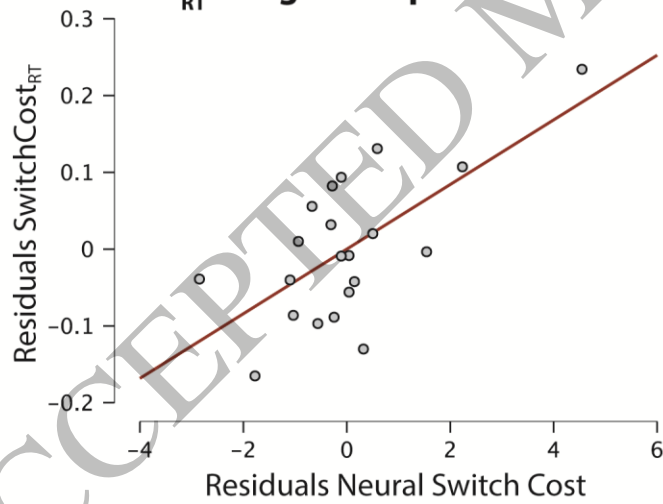


Figure 4
156x177 mm (.74 x DPI)

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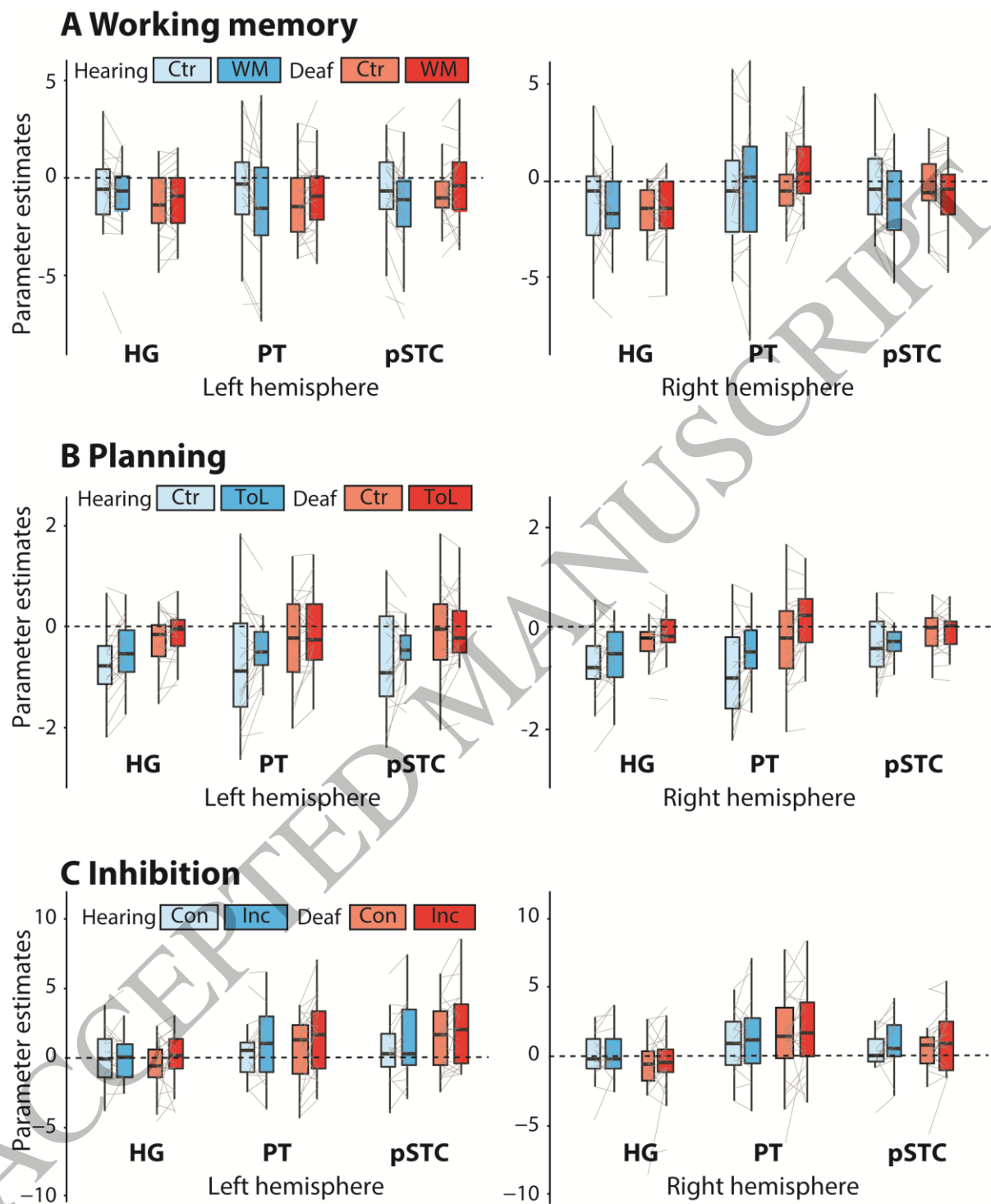


Figure 5
159x193 mm (.74 x DPI)

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