Sensory experience modulates the reorganisation of temporal auditory regions for executive processing

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Abstract

Crossmodal plasticity refers to the reorganisation of sensory cortices in the absence of their main sensory input. Understanding this phenomenon provides insights into brain function and its potential for change and enhancement. Using fMRI, we investigated how early deafness and consequent varied language experience influence crossmodal plasticity and the organisation of executive functions (EF) in the adult brain. Results from four visual EF tasks (working memory, switching, planning, inhibition) show that, as a function of the degree of deafness, deaf individuals specifically recruit "auditory" regions during switching. This recruitment correlates with performance, highlighting its functional relevance. We also observed recruitment of auditory temporal regions during planning, but only in deaf individuals with the highest language scores, suggesting differential use of linguistic skills to support EF. Our results show executive processing in typically sensory regions, suggesting that the development and ultimate role of brain regions are influenced by perceptual environmental experience.

Introduction

Understanding the impact of deafness on brain organisation reveals the effect that sensory developmental experience has on brain structure and function, and how they are differentially affected by nature and nurture. Previous research has focused on how deafness affects sensory processing and the reorganisation of sensory areas, but less is known about how it modulates higher-order cognitive processes. Language and executive processing are strongly linked (Figueras et al., 2008; Akbar et al., 2013; Woodard et al., 2016), and the study of cognition in deaf individuals can provide unique insights into the nature of this relationship, given the great heterogeneity in language experience and proficiency in this population. Here we study executive processing in deaf individuals to understand how early sensory and language experiences modulate crossmodal plasticity and the organisation of cognitive networks in the human brain.

What is the role of the deaf auditory cortex in cognition?

Executive functions (EF) refer to a set of cognitive processes responsible for the performance of flexible and goal-directed behaviours which allow individuals to act in a complex and changing environment (Baddeley and Hitch, 1994; Baddeley, 2002; Ridderinkhof et al., 2004; Gazzaley and D'Esposito, 2007; Diamond, 2013). EF have been widely associated with activity in frontoparietal areas (D'Esposito and Grossman, 1996; Gilbert and Burgess, 2008). These regions are thought to be specialised in representing abstract and task-related information (Christophel at al., 2017), maintaining behavioural goals in mind, filtering distractors (Ku et al., 2015), and performing top-down modulation on sensory regions in the service of attentional goals and task performances (Zanto et al., 2011). On the other hand, sensory regions, such as the auditory and visual cortices, are usually considered to preferentially process lower-level perceptual features and to contribute to the storage of representations of these features in working memory (Zanto et al., 2011; Ku et al., 2015; Christophel at al., 2017). However, the study of deafness and blindness suggests that this preference might be at least partially driven by environmental sensory experience, given that reorganisation for cognitive processing has been observed in sensory areas of deaf and blind individuals (Röder et al., 2000, 2002; Amedi et al., 2003, 2004; Buchsbaum et al., 2005; Bonino et al., 2008; Bedny et al., 2011; Park et al., 2011; Watkins et al., 2012; Ding et al., 2015; Cardin et al., 2018; Loiotile and Bedny, 2018; Rimmele et al., 2019). For

example, previous studies have shown recruitment for visual working memory in the posterior superior temporal cortex (pSTC) of deaf individuals (Buchsbaum et al., 2005; Ding et al., 2015; Cardin et al., 2018), suggesting a change in function in this area from auditory to cognitive processing as a consequence of deafness. While crossmodal plasticity usually refers to the adaptation of sensory brain regions to processing information from a different sensory modality (Rauschecker, 1995, 2002; Kral, 2007; Merabet and Pascual-Leone, 2010; Frasnelli et al., 2011; Heimler et al., 2015; Cardin et al., 2020a, 2020b; Ricciardi et al., 2020), these working memory responses in pSTC seem to suggest that in the absence of early sensory stimulation, a sensory region can change its function as well as the sensory modality to which it responds (Bedny, 2017; Cardin et al., 2020b). In addition, evidence suggests that auditory areas in deaf people are functionally connected to frontal regions involved in working memory, potentially being part of the same cortical network for EF and cognitive control (Ding et al., 2016; Cardin et al., 2018). Together, these findings suggest that the nature of the neural circuitry engaged in EF and cognitive control may be modulated by early sensory experience. Our first aim in this study is to understand the role of the auditory cortex in cognition in deaf individuals and the effect of sensory experience on the reorganisation of cognitive networks. The recruitment of auditory regions during visual working memory in deaf individuals could reflect a role in cognitive control, in line with what is generally found in the frontoparietal network; or it could also reflect involvement in a specific executive subcomponent that allows successful control, updating, manipulation, and storage of information (e.g. attentional shifts, inhibitory control). It could also reflect the storage of relevant sensory features, as has been observed in other sensory regions (Druzgal and D'Esposito, 2001; Feredoes et al., 2011). To dissociate between these hypotheses and understand the role of the deaf auditory cortex in cognition, we measured the recruitment of these regions during a range of tasks tapping into different subcomponents of executive function.

Does language modulate crossmodal plasticity and executive processing?

The study of deafness also allows us to investigate how early language experience impacts EF and brain reorganisation. This is due to the great heterogeneity in language experience and proficiency in this population. Deaf children of deaf parents are usually exposed to sign language from birth, and acquire language following similar developmental milestones to those of hearing children learning a spoken language. However, most deaf children are born

to hearing parents (~95%) (Moores, 2001; Mitchell and Karchmer, 2004) who usually do not know a sign language. In these cases, the onset of language acquisition varies but is typically delayed, with negative consequences for its development both in the signed and spoken modality (Mayberry, 2007; Cormier et al., 2012b; Humphries et al., 2012; Hall et al., 2019). Thus, in many cases, the different sensory experience of deaf individuals is accompanied by a delay in language acquisition and language deprivation (Humphries et al., 2012). This relationship between auditory and language experience has been a confound in many neuroscience, behavioural, and clinical studies (see Lyness et al. (2013) for a review), and language deprivation effects have been at times confounded as auditory deprivation effects. However, if language experience is measured or controlled, both in the signed and spoken modality, it can help us understand how language shapes the organisation of EF networks in the adult brain. This is a question that is difficult to study in the brain of hearing individuals because language is usually acquired to a high level of proficiency through environmental exposure. Atypical populations, including those with developmental language disorders, have helped in informing this relationship (e.g. Hughes, 2006; Marton, 2008; Akbar et al., 2013; Bishop et al., 2014), but in these populations, there are usually underlying neurological factors that could also impact cognitive function and neural organisation. In contrast, deaf children are fully able to acquire language within its critical period through the same milestones and to the same level of fluency as hearing children (Schlesinger and Meadow-Orlans, 1972; Newport and Meier, 1985; Emmorey, 2001; Morgan and Woll, 2002; Mayberry and Squires, 2006), and it is only due to lack of environmental exposure that this is not achieved (Mayberry, 2007, 2010; Cormier et al., 2012b; Humphries et al., 2012; Hall et al., 2019). Previous behavioural studies in deaf children have shown that language deprivation, and not deafness *per se*, negatively impacts EF (Kalback, 2004; Figueras et al., 2008; Remine et al., 2008; Marshall et al., 2015; Botting et al., 2017). It is also known that late language acquisition can impact the reorganisation of auditory areas and the neural substrates of language processing (Neville and Bavelier, 1998; MacSweeney et al., 2008a,b; Mayberry et al., 2011; Cardin et al., 2013; Ferjan Ramirez et al., 2014, 2016; Cardin et al., 2016; Twomey et al., 2017), but it is not known what effect it has on neural executive processing. Revealing the effect of language experience on executive processing in the brain will provide unique insights into the nature and mechanisms of this relationship. To achieve this, here we measured signed and spoken language proficiency in a group of deaf adults with varied language backgrounds to study

the effect of modality-independent language proficiency on EF processing and crossmodal plasticity.

The present study

Our overarching aim is to investigate whether sensory experience and language proficiency have a modulatory effect on behavioural performance and neural processing during EF tasks. Specifically, we aim to:

1) understand the role of the auditory cortex of deaf individuals in executive processing,
2) understand the effect of sensory experience on the function of frontoparietal regions,
3) investigate how different language experiences in childhood relate to executive processing, and how it manifests in the mature brain.

To achieve these, deaf and hearing individuals took part in an fMRI experiment including visual tasks that tapped into different EF: working memory, planning, switching, and inhibition (Figure 1). To study the effect of language on EF, we recruited a group of deaf participants with different language backgrounds, reflecting the heterogeneity observed in deaf communities, with varied proficiency and age of language acquisition. In this group, we measured grammaticality judgements in signed and spoken language and combined them into a single, modality-independent language proficiency measure which was used as a covariate in the analysis of behavioural and neural responses (see Methods).

If the functional reorganisation in the deaf auditory cortex applies to multiple different executive control functions, we would expect all four EF tasks to recruit temporal regions in deaf participants. However, if deaf auditory areas are involved in specific subcomponents of executive processing, these regions will be differentially activated by each of the tasks. If the strength of the neural activity is correlated with performance in the tasks, it will further show that crossmodal plasticity has tangible influences on behaviour (Lomber et al., 2010; Pavani and Bottari, 2012; Bottari et al., 2014).

Furthermore, differences in responses between deaf and hearing individuals in frontoparietal regions typically involved in cognitive control will show that early sensory experience also affects the organization of EF networks.

Finally, we hypothesise that modality-independent language proficiency will predict behavioural performance and neural response in EF tasks in deaf adults.

Results

Behavioural results

Group differences

fMRI scans were collected while deaf (N=25) and hearing (N=20) individuals performed four different EF tasks (Figure 1): working memory, planning, switching, and inhibition. The tasks were designed so that each had one condition with higher executive demands (Higher Executive Function condition; HEF) and one with lower demands (Lower Executive Function condition; LEF) (see Methods and Figure 1 for details). Behavioural results from all tasks are shown in Figure 2A-D. To explore differences in performance between groups, we conducted 2 x 2 repeated-measures ANOVAs for each task, with either accuracy or reaction time (RT) as the dependent variable, between-subjects factor group (hearing, deaf), and within-subjects factor condition (HEF, LEF). Results show a significant main effect of condition for both accuracy and RT in all tasks (Table 1A). The group of deaf individuals also had significantly slower RTs in all tasks (main effects of group in Table 1A).

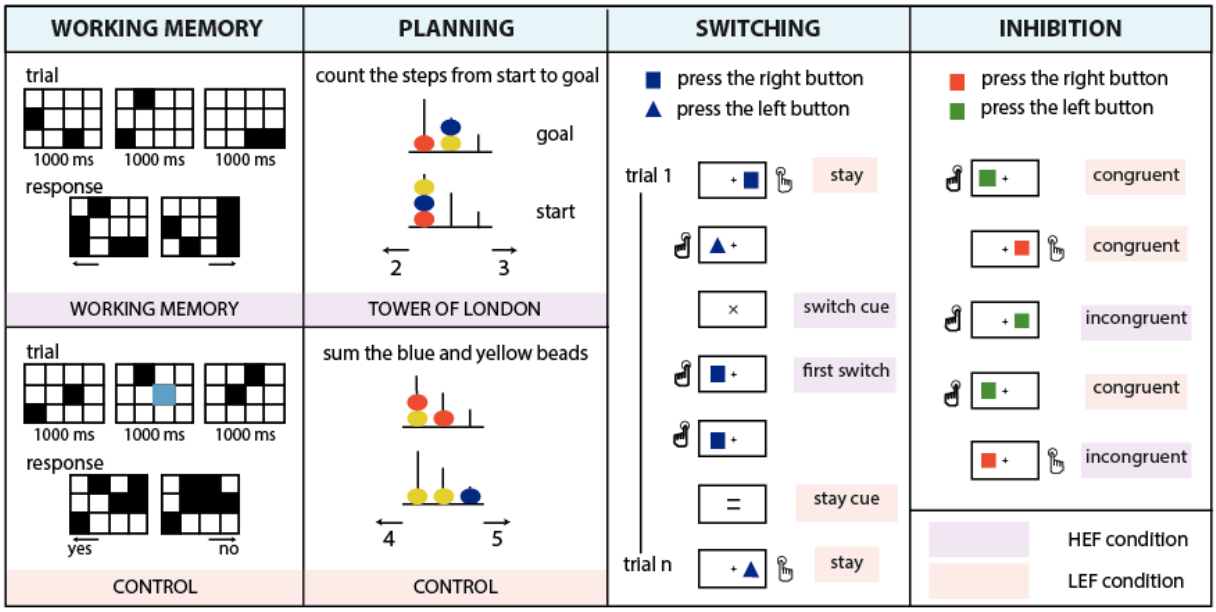


Figure 1. Executive function tasks. Each task had a higher executive demands condition (HEF=Higher Executive Function, purple) and a lower executive demands condition (LEF=Lower Executive Function, peach). See Methods for details of the design.

In the inhibition task, there was also a significant condition × group interaction ($F_{1,35}$=9.54, p=0.004). A post-hoc t-test revealed that the deaf group was significantly slower in the congruent condition (t_{35}=2.72, p=0.01). This condition × group interaction in RT is also reflected in a significant difference between groups in the Simon effect ($RT_{incongruent}$–$RT_{congruent}$) (t_{35}=-2.48, p=0.02; Figure 2D; Table 1B), which was smaller in the deaf group (mean=19 ms; SD=17ms) than in the hearing group (mean=33ms; SD=15ms).

Switching was the only task where there was a significant main effect of group on accuracy ($F_{1,41}$=5.16, p=0.03) and a condition × group interaction ($F_{1,41}$=5.75, p=0.02). A post-hoc Mann-Whitney test revealed that the deaf group was significantly less accurate in the switch condition (U=124, p=0.01). The difference in the accuracy switch cost ($\%errors_{switch}$–$\%errors_{stay}$) (Table 1B) confirms this pattern, with the deaf group (mean=10.60ms; SD=9.68ms) having a larger accuracy switch cost than the hearing group (mean=4.18ms; SD=7.53ms; t_{41}=2.40, p=0.02; Figure 2B).

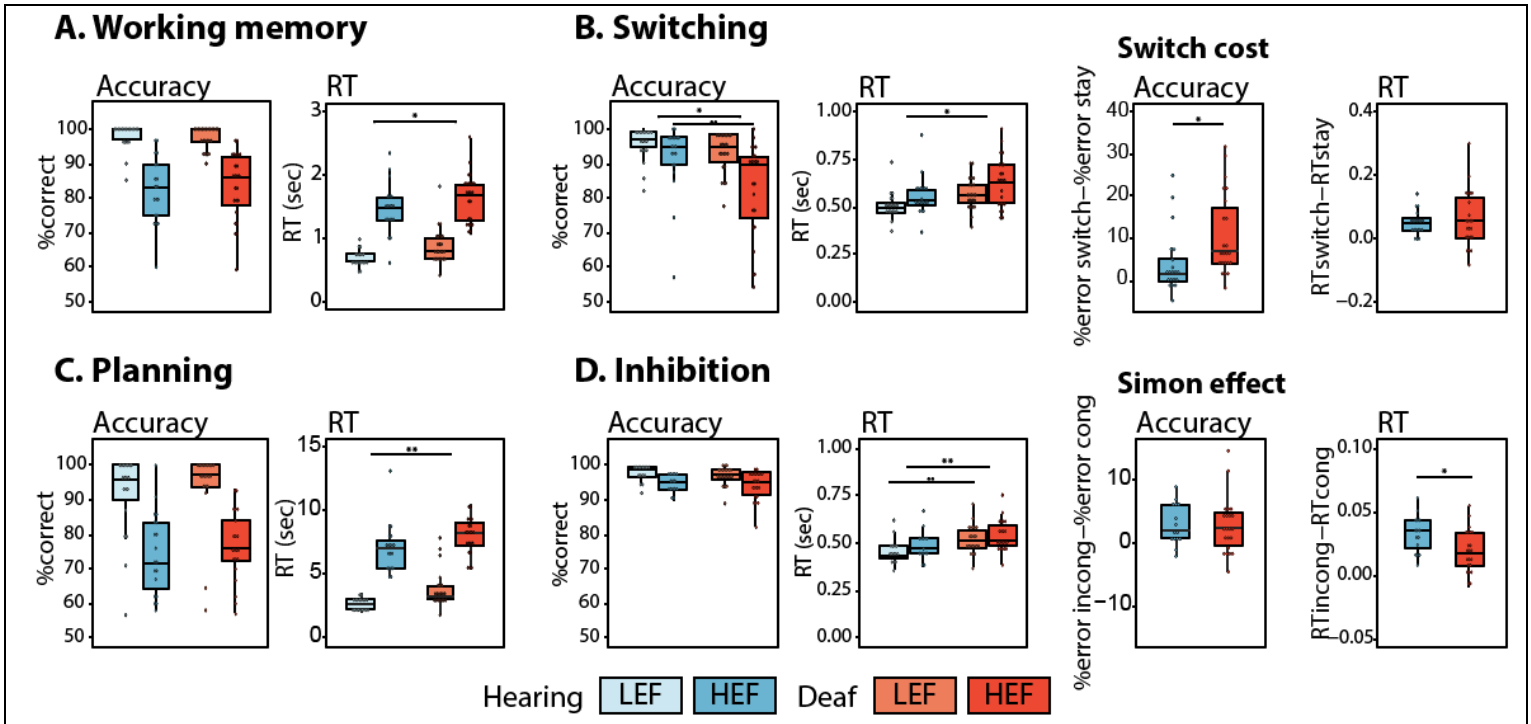


Figure 2. Behavioural performance. The figure shows average accuracy (%correct) and reaction time (seconds) for each task and condition in the hearing and the deaf groups. It also shows the average switch costs and Simon effects for both accuracy and reaction time in each group. The accuracy switch cost and Simon effect are calculated and plotted using %error instead of %correct so that larger values indicate an increase in cost. Only the first trial of the switch block was included in the HEF condition. The bold lines in the box plots indicate the median. The lower and upper hinges correspond to the first and third quartiles. Differences between conditions were statistically significant (p<0.05) for all tasks in both groups (not shown). Values for all behavioural results can be found in Table S1. **p<0.01; *p<0.05.

Table 1A. Results from repeated-measures ANOVAs on behavioural performance

	WM		**Switching**		**Planning**		**Inhibition**	
	Accuracy							
	F (df)	*p*	*F (df)*	*p*	*F (df)*	*p*	*F (df)*	*p*
Condition	**91.52 (1,41)**	**<0.001**	**30.51 (1,41)**	**<0.001**	**46.07 (1,38)**	**<0.001**	**19.15 (1,35)**	**<0.001**
Group	0.07 (1,41)	0.80	**5.16 (1,41)**	**0.03**	0.83 (1,38)	0.37	0.70 (1,35)	0.41
Condition × Group	0.29 (1,41)	0.59	**5.75 (1,41)**	**0.02**	0.02 (1,38)	0.88	0.04 (1,35)	.856
	Reaction time							
	F (df)	*p*	*F (df)*	*p*	*F (df)*	*p*	*F (df)*	*p*
Condition	**197.55 (1,41)**	**<0.001**	**27.53 (1,41)**	**<0.001**	**240.29 (1,38)**	**<0.001**	**102.28 (1,35)**	**<0.001**
Group	**4.97 (1,41)**	**0.03**	**5.14 (1,41)**	**0.03**	**8.57 (1,38)**	**0.03**	**9.45 (1,35)**	**0.004**
Condition × Group	0.02 (1,41)	0.87	0.24 (1,41)	0.62	0.31 (1,38)	0.62	**5.29 (1,35)**	**.03**

Factors in the analysis were: condition (HEF, LEF) and group (hearing, deaf). Bold numbers indicate significant effects.

Table 1B. Results from ANOVAs on the switch costs and the Simon effects

	Switching		**Inhibition**	
	Accuracy			
	Switch cost		**Simon effect**	
	F (df)	*p*	*F (df)*	*p*
Group	**5.751 (1,41)**	**0.02**	0.04 (1, 35)	0.85
	Reaction time			
	Switch cost		**Simon effect**	
	F (df)	*p*	*F (df)*	*p*
Group	0.256 (1,41)	0.62	**6.140 (1,35)**	**0.02**

Switch costs and Simon effects for either accuracy and RT were the dependent variables in the ANOVAs. Group was set as a fixed factor. Bold numbers indicate significant effects.

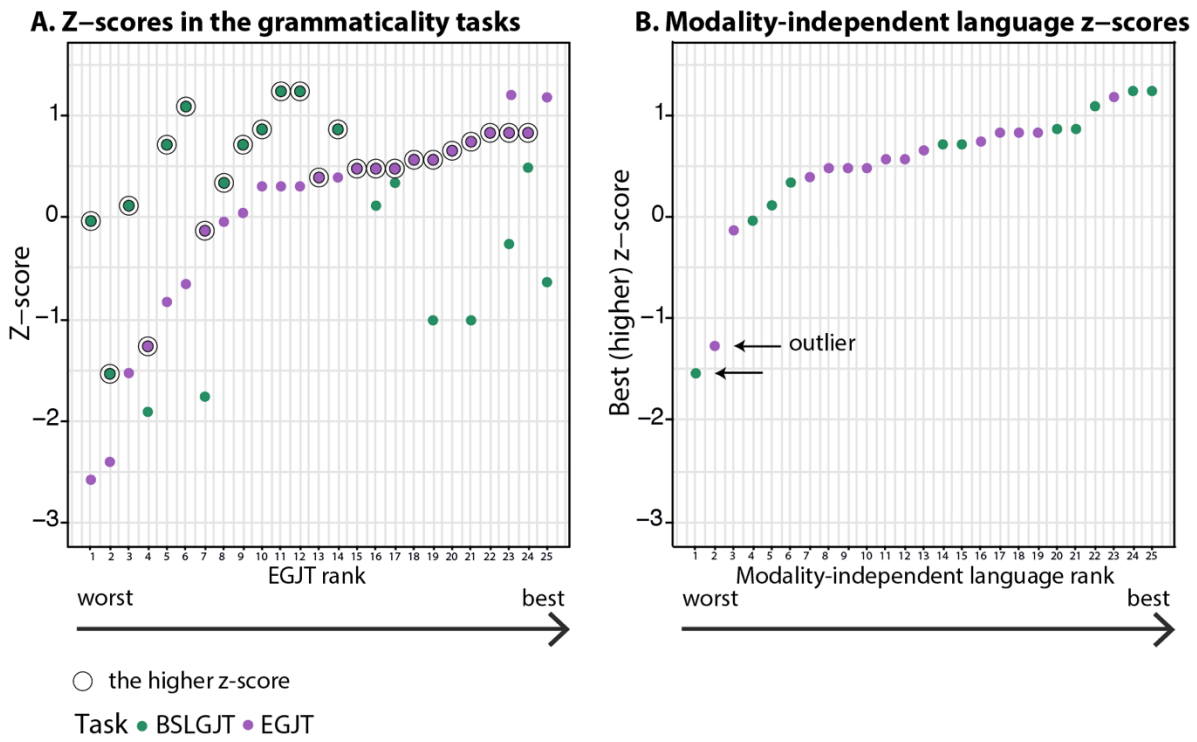


Figure 3. Performance in the language tasks in the deaf group. A. Language z-scores in the English Grammaticality Judgement Task (EGJT) and BSL Grammaticality Judgement Task (BSLGJT) in the deaf group with participants ranked on the x-axis by their EGJT rank. Black circles indicate the z-score chosen for the combined modality-independent language score. English monolingual participants performed only the EGJT. **B.** Final modality-independent language z-scores. Two participants with the lowest z-scores were removed from all language-related analyses.

Effect of language on behavioural performance in the deaf group

To test whether the variability in behavioural performance in the deaf group can be explained by their unique language experience, we further investigated the relationship between EF and language proficiency. This analysis was conducted only in the group of deaf individuals, as the variability in language proficiency observed in deaf individuals is not typically found in the hearing population in the absence of underlying neurological conditions or extreme social isolation. We used results from English and BSL grammaticality judgement tasks (EGJT and BSLGJT) to create a single, modality-independent measure of language proficiency in the deaf group (see Methods). Accuracy scores in the EGJT (%correct; mean=83.48, SD=11.41, N=25) and BSLGJT (mean=78.45, SD=13.30, N=20) were transformed into z-scores separately for each test (Figure 3A). For each participant, the

EGJT and BSLGJT z-scores were then compared and the higher one was chosen for a combined modality-independent language proficiency score (Figure 3B). Data from two participants whose performance clearly deviated from that of the group (>2 SD from the mean) were removed from the analysis that included language as a covariate (see outliers in Figure 3B).

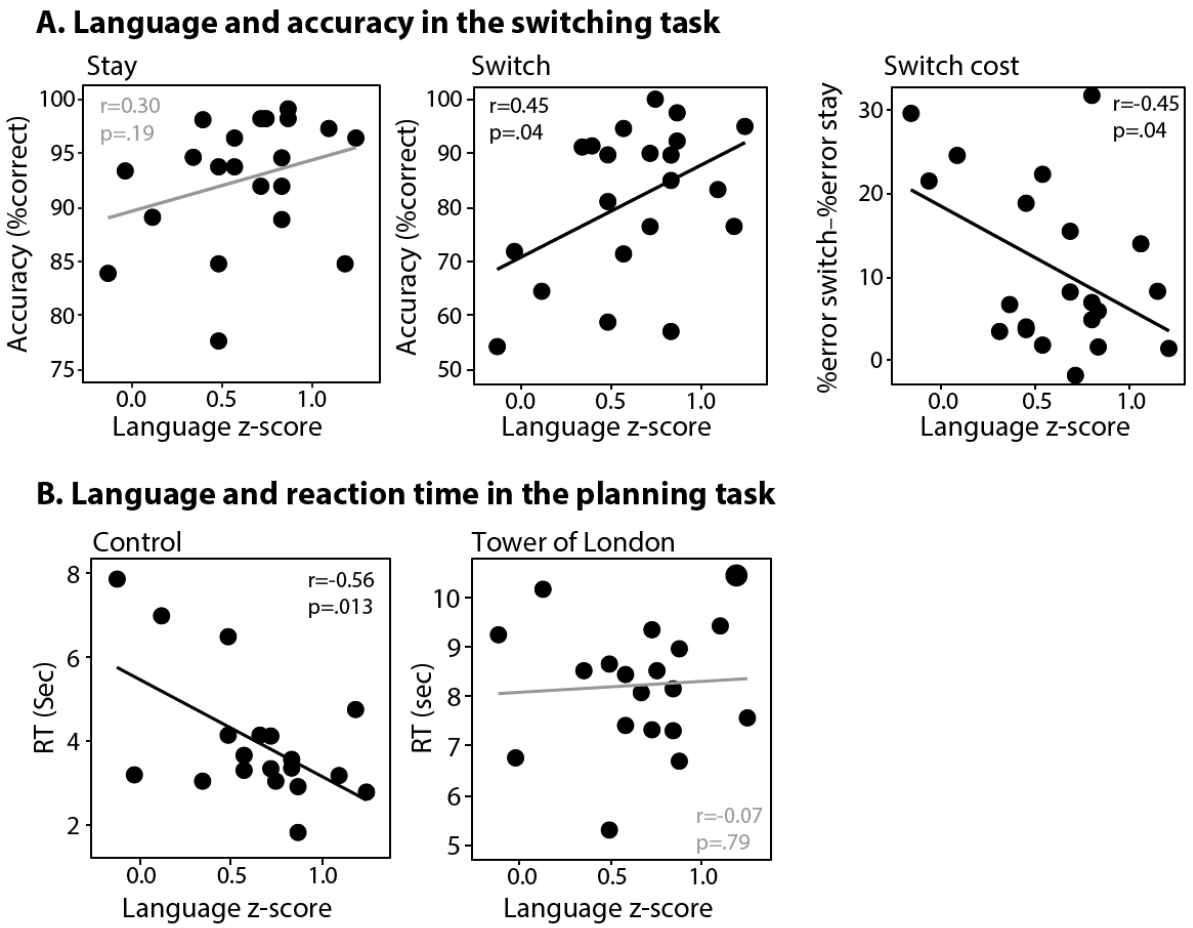


Figure 4. The relationship between language proficiency and behavioural performance in the deaf group. A. Correlations between accuracy (%correct and switch cost) and language z-scores in the switching task in the deaf group. **B.** Correlations between RT and language z-scores in the planning task in the deaf group.

For each task, we performed ANOVAs with condition (LEF, HEF) as a factor and language z-score as a covariate. The analysis revealed a significant condition x language z-score interaction in the switching task ($F_{1,19}$=4.82, p=0.04). A post-hoc analysis showed that there was a significant positive correlation between language z-scores and accuracy in the switch condition (r=0.45, p=0.04) but not in the stay condition (p>0.05) (Figure 4A). This correlation suggests that participants with higher language proficiency scores were more accurate in the switching condition, which is also reflected in a significant correlation between language z-scores and the accuracy switch cost (r=0.45, p=0.04) (Table S2B, Figure 4A).

In the planning task, we found a significant condition x language z-score interaction ($F_{1,17}$=7.23, p=0.02) for RT. A post-hoc analysis showed a significant negative correlation between RT in the control condition and language z-scores (r=-0.56, p=0.01) (Figure 4B).

There were no significant main effects or interactions with language proficiency in the working memory and inhibition tasks (Table S2A).

Neuroimaging results

The main effect of condition across groups

Figure 5 shows brain activity for each EF task and condition averaged across groups. There were significantly stronger activations in the HEF condition in the working memory, planning, and switching tasks (Table S3, Figure 5). These included commonly found activations in frontoparietal areas, such as dorsolateral prefrontal cortex (DLPFC), frontal eye fields (FEF), pre-supplementary motor area (pre-SMA), and intraparietal sulcus (IPS). In the inhibition task, the HEF incongruent condition resulted in stronger activation in IPS and left FEF, but there were no significant differences between conditions (Figure 5D).

Group differences and language effects

We conducted a region of interest (ROI) analysis to investigate differences between groups in executive processing and their relationship to behavioural performance and language (in tasks where language correlated with behaviour). We limited our statistical inferences to two predefined sets of ROIs: temporal auditory regions and frontoparietal areas (see Methods). Temporal ROIs included are Heschl's gyrus (HG), the planum temporale (PT), and the

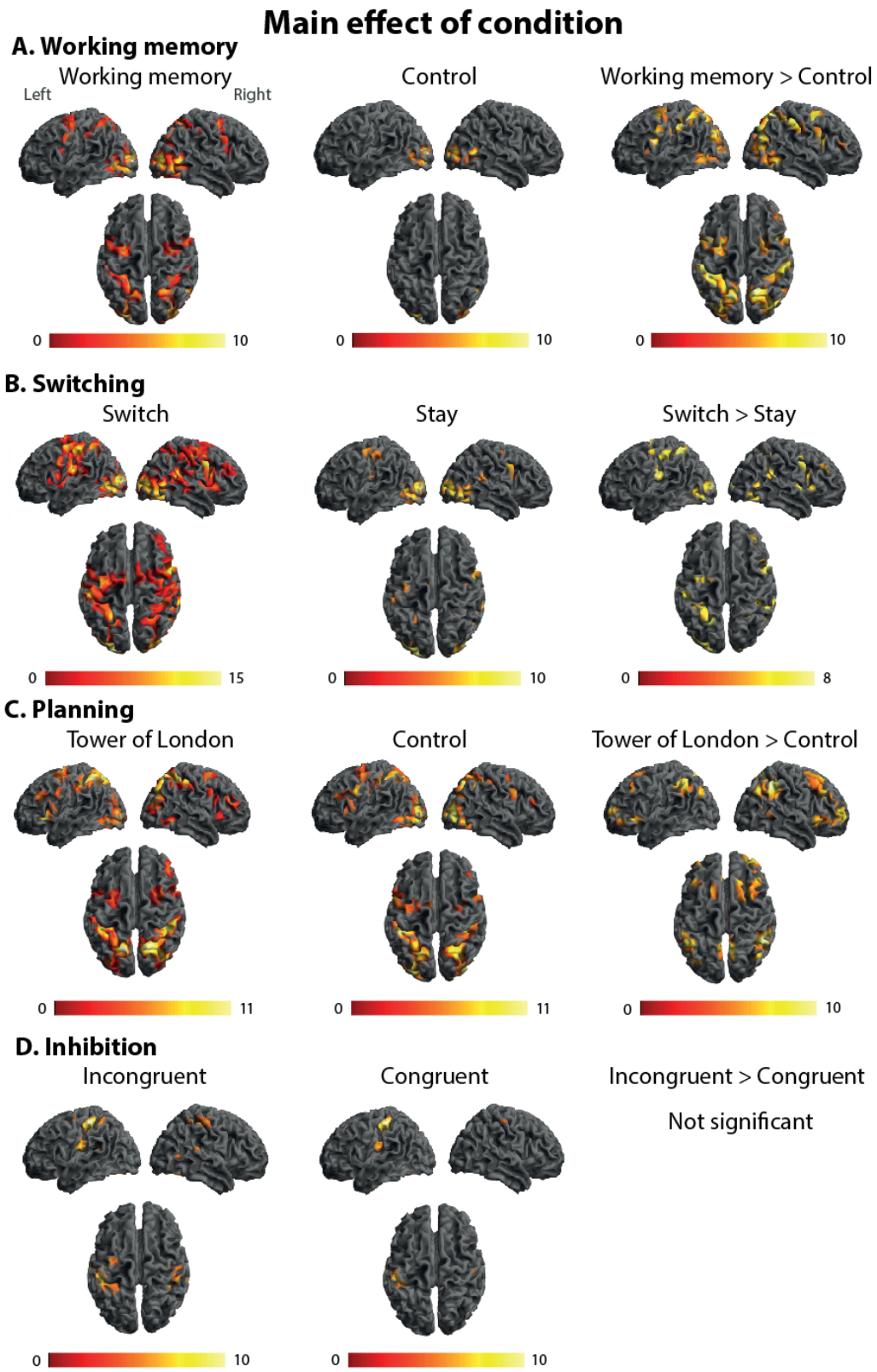


Figure 5. Whole-brain main effects of condition in each EF task. Contrasts calculated across both groups. All contrasts are displayed at $p<0.05$ (FWE-corrected). Colour bars represent z-scores.

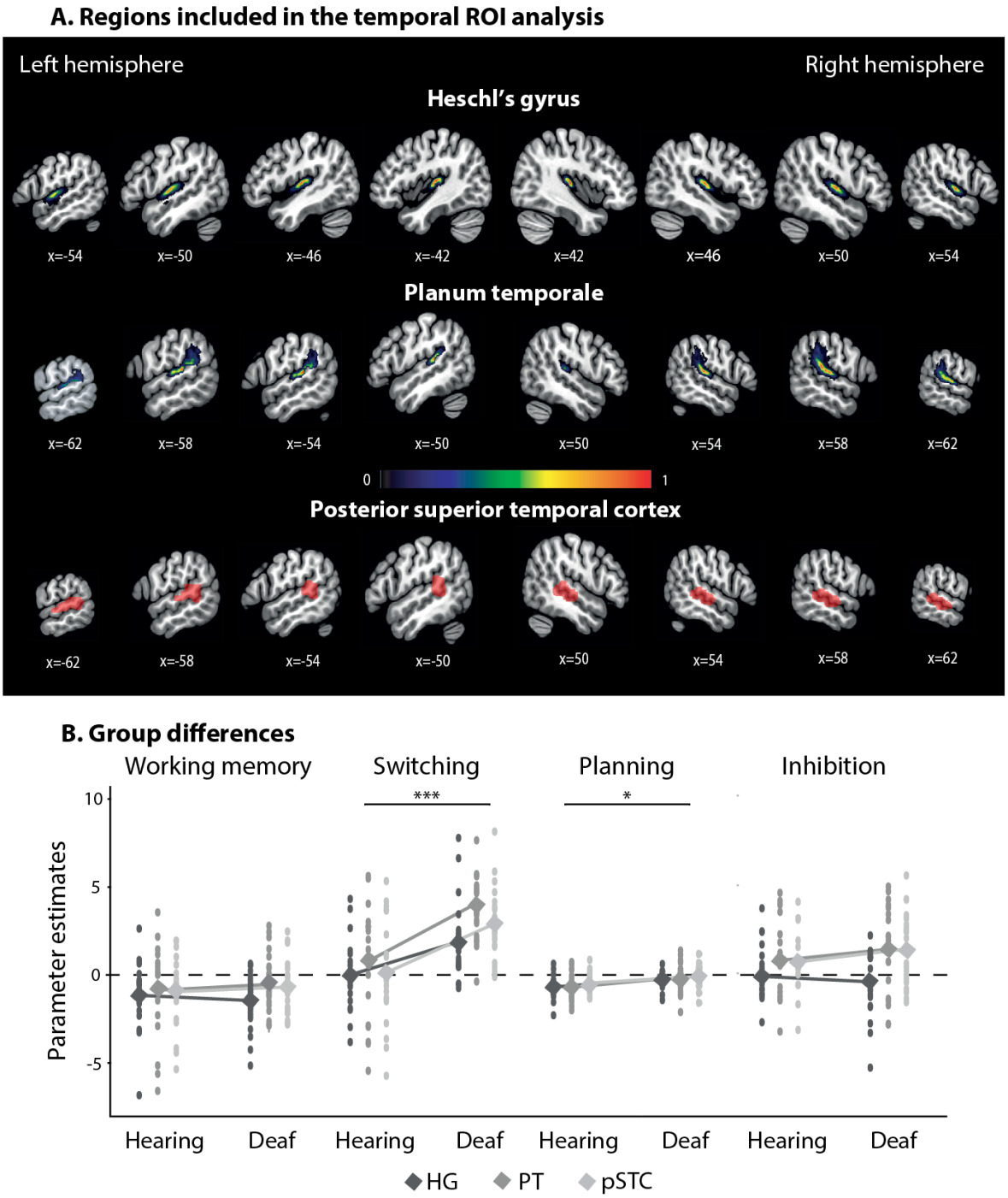


Figure 6. Temporal ROIs analysis summary. A. Temporal regions included in the analysis: Heschl's gyrus (HG), the planum temporale (PT), and the superior temporal cortex (pSTC). HG and PT were defined anatomically, in a subject-specific manner, using the FreeSurfer software package. The figure shows the overlap of all subject-specific ROIs. Common voxels between left PT and left pSTC have been subtracted from left PT (see Methods). pSTC was defined functionally, based on the findings of Cardin et al. (2018) (see Methods). **B.** fMRI group effects in temporal ROIs. ***$p<0.001$; *$p<0.05$.

posterior superior temporal cortex (pSTC) (Figure 6A). The frontoparietal ROIs included are the dorsolateral prefrontal cortex (DLPFC), frontal eye fields (FEF), the pre-supplementary motor area (pre-SMA), the insula, and the superior parietal lobule (SPL) (Figure S1). Whole-brain effects of condition are also shown to aid the description of significant effects.

Results of group averages in auditory temporal ROIs can be found in Figure 6B. Differences and interactions between groups are discussed below separately for each task, starting with switching, where we observed the strongest activation of temporal ROIs in the deaf group.

Switching

Temporal ROIs. The analysis of temporal ROIs showed increased activations during the switching task in the deaf group (Figures 6, 7A). A repeated-measures ANOVA with between-subjects factor group (hearing, deaf) and within-subjects factors condition (switch, stay), ROI (HG, PT, pSTC) and hemisphere (left, right), revealed the following significant results:

a) main effect of group ($F_{1,41}$=14.48, p<0.001), due to significantly higher activations in temporal regions in the deaf group (HG: t_{41}=2.99, p=0.005; PT: t_{41}=3.95, p<0.001; pSTC: t_{41}=3.65, p<.001) (Figure 6B);

b) group x condition interaction ($F_{1,41}$=4.75, p=0.03), due to higher activations in the deaf group during the switching condition (HG: t_{22}=2.57, p=0.02; PT: t_{22}=4.70, p<0.001; pSTC: t_{22}=4.51, p<0.001) and no significant differences between conditions in the hearing group (all p>0.5) (Figure 7A);

c) group x ROI interaction ($F_{1.93,79}$=3.42, p=0.04), indicating a significant difference in the activation observed between the deaf and hearing group across ROIs ($PT_{deaf\text{-}hearing}$=3.28 > $pSTC_{deaf\text{-}hearing}$ =2.78 > $HG_{deaf\text{-}hearing}$ =1.98) (Figure 7A).

To investigate whether these interactions were reflected in differences in behavioural performance, we included RT and accuracy switch cost as covariates in the analysis. When RT switch cost was included as a covariate, there was a significant interaction between switch cost and: 1) group ($F_{1,39}$=7.78, p=0.008); 2) group x condition ($F_{1,39}$=8.00, p=0.007); and 3) group x condition x ROI x hemisphere ($F_{1.99,77.6}$=4.58, p=0.01). To investigate these, correlations coefficients between the behavioural RT switch cost and the neural switch cost ($BOLD_{switch}$–$BOLD_{stay}$) (see Methods) were calculated for each ROI and group (Figure 7B). In the deaf group, these revealed a positive correlation between behavioural switch cost and

neural switch cost in left HG (r=0.58, p=0.007), right pSTC (r=0.47, p=0.02), and right PT (r=0.53, p=0.009), with an overall positive correlation trend in all other ROIs (positive values in purple in Figure 7B; see also Figure S2A). The opposite overall trend was found in the hearing group, with significant negative correlations in left pSTC (r=-0.53, p=0.02) and right HG (r=-0.56, p=0.01) (negative values in green in Figure 7B; Figure S2A).

With accuracy switch cost included as a covariate, we found a significant interaction between accuracy switch cost and: 1) group ($F_{1,39}$=4.28, p=0.04); 2) group and condition ($F_{1,39}$=7.81, p=0.008). We also found a significant effect of group ($F_{1,39}$=5.26, p=0.03). Post-hoc correlations revealed that these interactions were driven by negative correlations in left PT (r=-0.45, p=0.05) and left pSTC (r=-0.53, p=0.02) in the hearing group (Figure S2B). No significant correlations were found in the deaf group.

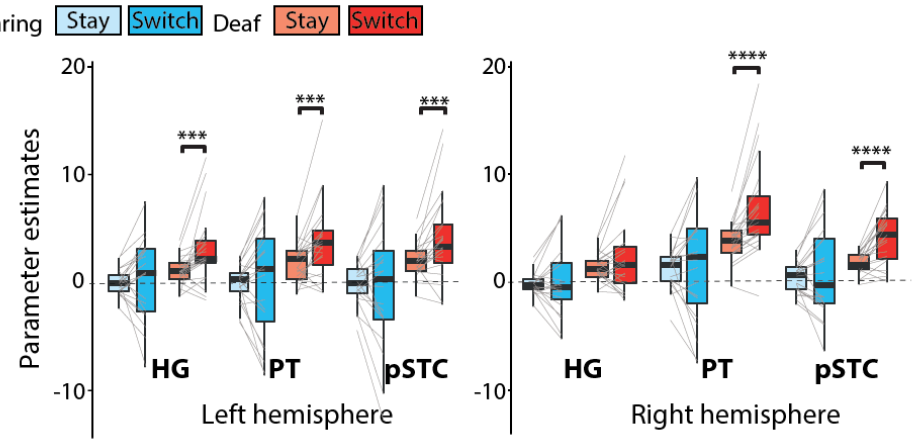
The results observed in HG suggest that plastic changes occur in primary auditory areas. However, HG contains at least three distinct cytoarchitectonic areas: Te1.0, Te1.1, and Te1.2. Based on its granularity (Morosan et al., 2001; Hackett, 2011) and its anatomical position (Dick et al., 2012), Te1.0 is the region that is more likely to contain the primary auditory cortex. Analysis of subject-specific Te1.0 showed results that were qualitatively comparable to those in HG. There was a significant correlation between RT switch cost and neural switch cost in the left Te1.0 in the deaf group (r=0.42, p=0.04) and a negative correlation in the right Te1.0 of the hearing group (r=-0.55, p=0.01).

Frontoparietal ROIs. A significant main effect of group ($F_{1,41}$=4.39, p=0.05) driven by higher activations in the deaf group was also found in frontoparietal areas during the switching task (Figure S3). However, in contrast to the results found in temporal ROIs, there was no significant interaction between condition and group, and no significant correlation between behavioural and neural switch cost.

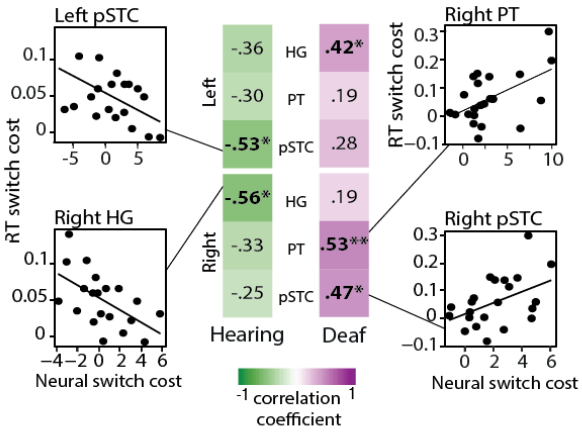
Whole-brain. The results of the ROI analysis were also apparent in the whole-brain, where there are different profiles of activity for the contrast [switch > stay] in the deaf and hearing groups (Table 2A, Figure 7D). These differences included activations for the deaf group along the right and left pSTC, which were absent in the hearing group. Group comparison revealed a significant main effect of group (p<0.05, FWE-corrected), with higher activations for the deaf group in the right calcarine sulcus, bilateral pSTC, and the bilateral middle precentral gyrus (Table 2B, Figure 7D).

Switching

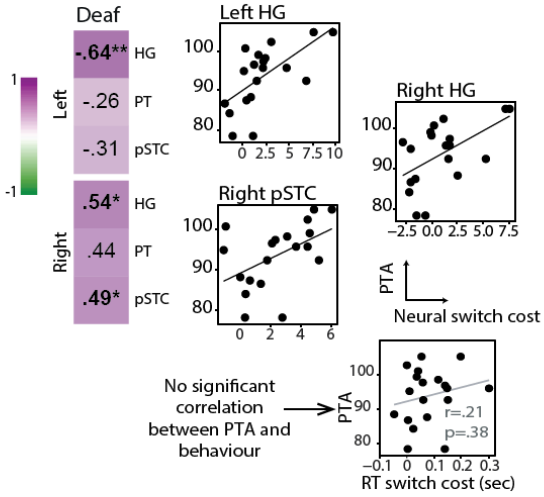
A. Neural activity in the temporal regions



B. Correlations between RT switch cost and neural switch cost



C. Correlations between PTA and neural switch cost



D. Whole-brain analysis

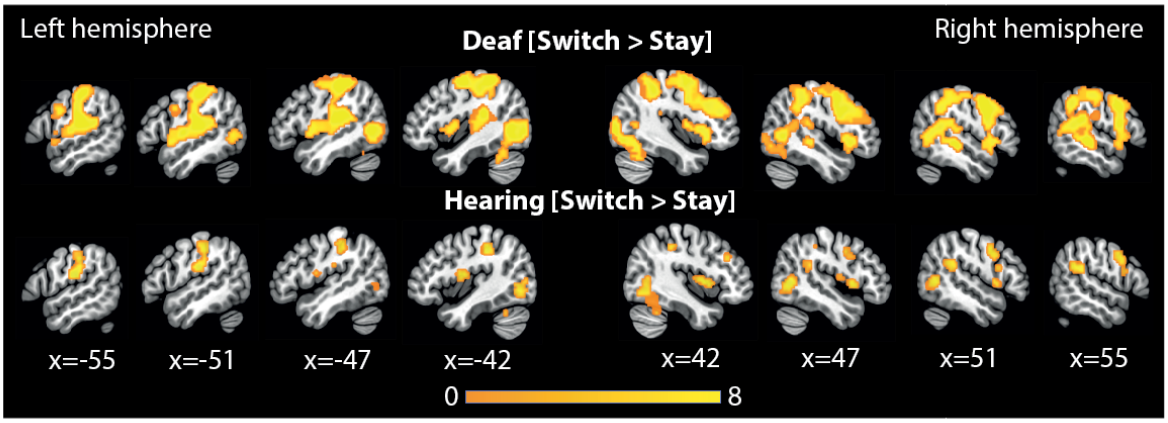


Figure 7.

Figure 7. Switching task analysis. A. Neural activity in temporal ROIs. ***p<0.005; ****p<0.001. **B.** Correlations between RT switch cost and neural switch cost in temporal ROIs. Correlation coefficients are colour-coded (green: negative; purple: positive. See the colour bar). Significant correlation coefficients are shown in bold. *p<0.05; **p<.01. L=left, R=right. HG=Heschl's gyrus, PT=the planum temporale, pSTC=the posterior superior temporal cortex. **C.** Correlations between PTA (pure-tone average) and neural switch cost in temporal ROIs in the deaf group. **D.** Whole-brain analysis: deaf [switch > stay] and hearing [switch > stay]. Contrasts displayed at p<0.001 for visualization purposes but all peaks significant at p<0.05 (FWE-corrected). Colour bars represent z-scores.

Language. The behavioural analysis showed a relationship between language proficiency and accuracy in the switching task in the group of deaf individuals. To understand whether language proficiency was also related to the level of recruitment of temporal regions during switching, we looked at the effect of language z-score as a covariate in our analyses. No significant effects of language were found in this analysis — neither in the temporal nor in the frontoparietal ROIs.

Effect of Degree of Deafness. To investigate whether the degree of deafness contributed to the extent of neural plasticity observed in temporal regions, we conducted a repeated-measures ANOVA on the neural activity in the deaf group using hearing threshold (pure-tone average; PTA) as a covariate. The factors included were condition (switch, stay), ROI (HG, PT, pSTC), and hemisphere (left, right). The analysis revealed a significant condition x PTA interaction ($F_{1,17}$=5.79, p=0.03) and a condition x ROI x PTA interaction ($F_{2,34}$=3.85, p=0.03). To explore these interactions further, we conducted a repeated-measures ANOVA with condition as a factor for each ROI separately. The ANOVAs revealed a significant condition x PTA interaction in HG ($F_{1,17}$=9.85, p=0.006), but not in the other two ROIs. Correlations between neural switch cost and PTA were significant in the left HG (r=0.64, p=0.003), right HG (r=0.54, p=0.02), and in the right pSTC (r=0.49, p=0.03) (Figure 7C).

Table 2A. Peak activations for the contrast [switch > stay] in the deaf and hearing groups

Name		**Deaf** [switch > stay] **Peak voxels**				**Hearing** [switch > stay] **Peak voxels**			
		z-score	*x*	*y*	*z*	*z-score*	*x*	*y*	*z*
Calcarine sulcus	L	6.79	-12	-97	2	-	-	-	-
	R	7.8	12	-94	-1	-	-	-	-
Extrastriate cortex	L	5.51	-45	-67	2	5.38	-36	-73	-10
	R	5.56	39	-85	-1	-	-	-	-
Superior parietal lobule	L	6.15	-36	-49	59	-	-	-	-
Posterior superior temporal cortex	L	4.5	-57	-40	17	-	-	-	-
	R	5.89	57	-25	-4	-	-	-	-
Frontal eye field	L	5.68	-39	-7	62	-	-	-	-
	R	5.60	51	5	44	-	-	-	-
Pre-supplementary motor cortex	R	5.41	0	5	47	-	-	-	-
Supramarginal gyrus	L	5.51	-51	-25	17	-	-	-	-
	R	5.1	57	-34	23	5.22	-54	-22	23
Insula	L	5.36	33	17	2	-	-	-	-
	R	-	-	-	-	4.62	39	2	5
Inferior frontal gyrus	R	5	57	8	17	-	-	-	-
Anterior prefrontal cortex	L	-	-	-	-	-	-	-	-
	R	4.93	33	47	26	-	-	-	-
Heschl's gyrus	L	4.51	-54	-10	8	-	-	-	-
Central operculum	L	4.5	-51	-7	5	-	-	-	-
Postcentral gyrus	L	6.36	-48	-31	53	4.54	-42	-34	41
Precentral gyrus	L	-	-	-	-	4.55	-39	-7	14
	R	4.88	36	-4	50	-	-	-	-
Fusiform gyrus	R	-	-	-	-	5.45	33	-58	-13

All values are significant ($p<0.05$, FWE) at peak level. L=left, R=right.

Table 2B. The main effect of group for switching

Name		[deaf > hearing] **Peak voxels**			
		z-score	*x*	*y*	*z*
Calcarine cortex	L	4.13*	-60	-40	14
Superior temporal cortex	R	5.95	15	-94	5
	R	4.49	66	-28	8
Middle precentral gyrus	B	3.99*	-3	-22	56

All values are significant ($p<0.05$, FWE) at peak level, except for those denoted by *, which were significant at the cluster level. L=left, R=right, B=bilateral.

Working memory

Temporal ROIs. In temporal ROIs, a repeated-measures ANOVA with within-subjects factor group (hearing, deaf) and fixed factors condition (working memory, control), ROI (HG, PT, pSTC) and hemisphere (left, right) revealed a significant condition × group interaction ($F_{1,41}$=6.43, p=0.01) in the working memory task. This effect was due to different trends of activity across groups and conditions. Specifically, the deaf group showed increased activity during the working memory condition, whereas the opposite trend was found in the hearing group (Figure 8A). Differences between conditions within each group were not significant (hearing: t_{18}=1.74, p=0.10; deaf: t_{23}=1.81, p=0.08). No significant main effect of group was found.

The lack of significant WM effects in the deaf group in temporal regions is potentially at odds with previous findings showing recruitment of pSTC regions for visual working memory in deaf individuals (Buchsbaum et al., 2005; Ding et al., 2015; Cardin et al., 2018). To investigate this discrepancy, we conducted exploratory t-tests separately for each ROI and each group (Figure 8B). These revealed increased activations in the deaf group during the WM condition only in the right PT (t_{23}=3.04, p=0.006; Figure 8B), and not in any of the other temporal ROIs.

Frontoparietal ROIs. Analysis of activity in frontoparietal regions showed a significant main effect of condition (Figure S4), but no significant main effect or interaction with group.

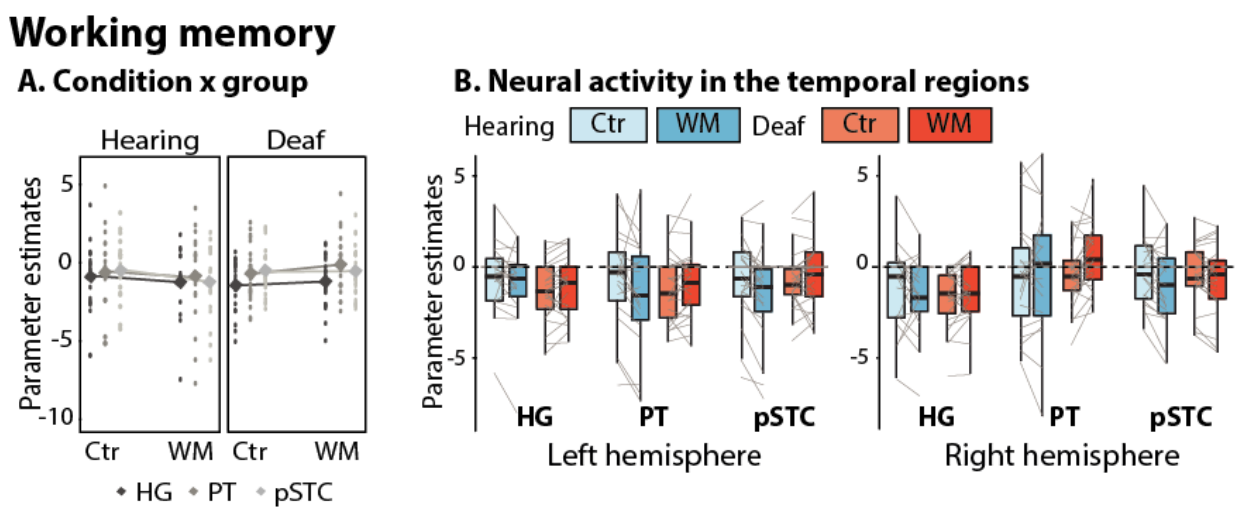


Figure 8. Temporal ROIs analysis for the working memory task. A. Condition x group interaction. **B.** Neural activity in temporal regions. Ctr=control, WM=working memory. HG=Heschl's gyrus, PT=the planum temporale, pSTC=the posterior superior temporal cortex.

Planning

Temporal ROIs. Analysis of temporal ROIs showed a significant main effect of group ($F_{1,38}$=5.85, p=0.02) (Figures 6B, 9A) in the planning task. This was driven by significant deactivations in the hearing group (t_{18}=-4.47, p<0.001) (Figure 6B, 9A), with no significant difference in activity from baseline in the deaf group (t_{20}=-1.309, p=0.205). No significant condition × group interaction was found.

Frontoparietal ROIs. Analysis of activity in frontoparietal regions showed a significant main effect of condition (Figure S5), but no significant main effect or interaction with group.

Language. To investigate the effect of language on the neural activity in the temporal ROIs during the planning task in the deaf group, we conducted a 3x2x2 repeated-measures ANOVA with condition (control, Tower of London) x ROI (PT, HG, pSTC), hemisphere (left, right) as factors, and language z-score as a covariate. This analysis revealed a significant ROI x language z-score interaction ($F_{2,34}$=8.01, p=0.001). To explore this interaction, we calculated correlation coefficients between language z-score and the neural activity for each combination of hemisphere and condition for each ROI (Figure 9B). There was a significant correlation between language z-score and neural activity in left PT in both the Tower of London condition (r=0.56, p=0.01) and the control condition (r=0.48, p=0.04) (Figure 9B) and between language z-score and neural activity in the right pSTC in the Tower of London condition (r=0.46, p=0.05) (Figure 9B). Correlations with neural activity in HG were not significant (Figure S6).

There was no significant main effect of language in the analysis of the frontoparietal regions in this task.

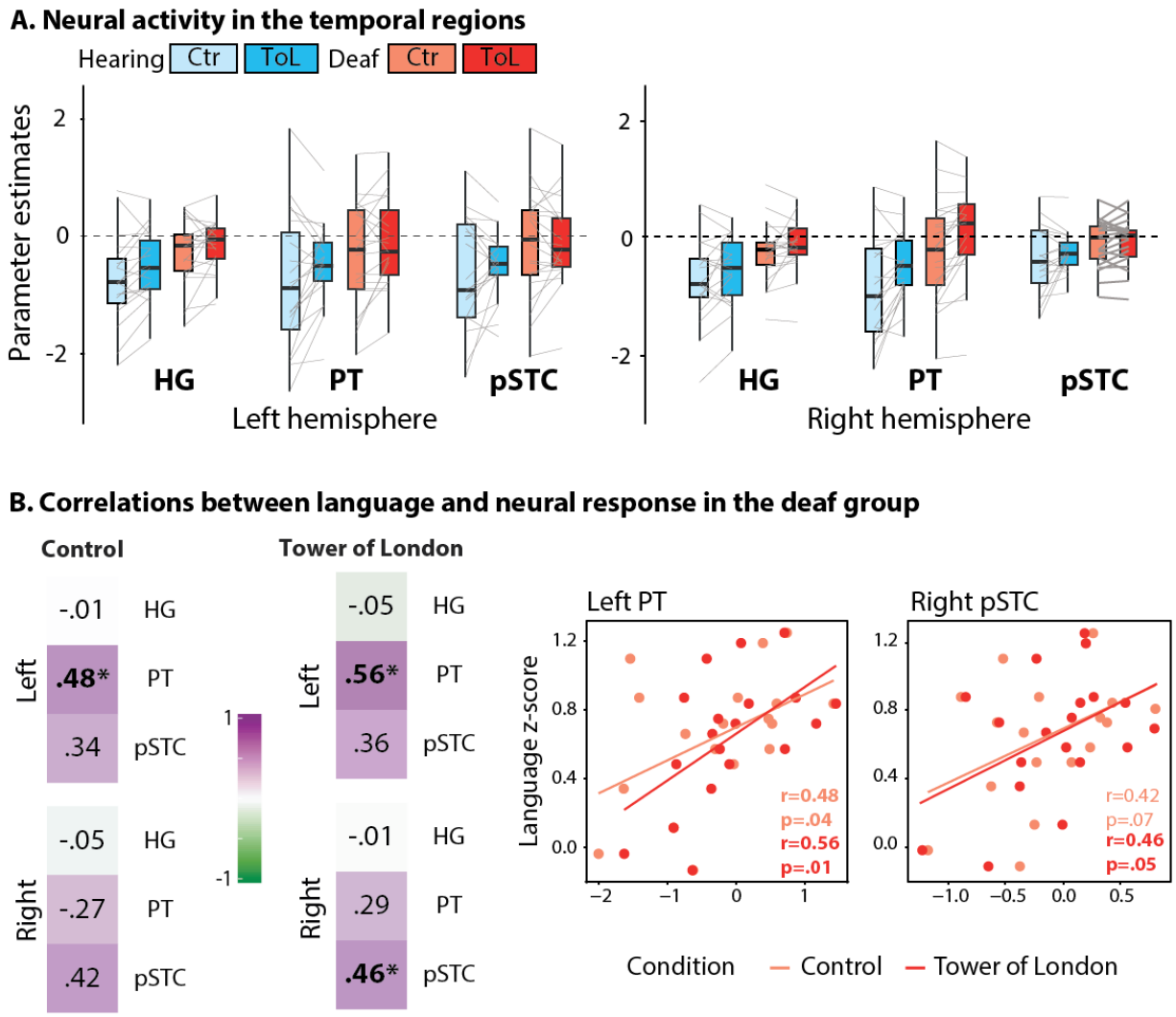


Figure 9. Temporal ROI analysis on planning. A. Neural activity in the temporal regions in both groups. **B.** Correlations between language and neural response in the deaf group. Ctr=control, ToL=Tower of London. HG=Heschl's gyrus, PT=the planum temporale, pSTC=the posterior superior temporal cortex.

Inhibition

Temporal ROIs. There was a significant interaction between ROI and group ($F_{1.89,66.05}$=3.92, p=0.03; Figure 10). There were no significant differences between groups in any ROI. Instead, the ROI x group interaction was driven by a main effect of ROI in the deaf group (higher activations for PT and pSTC than HG; Figure 6B), which was not present in the hearing group.

Frontoparietal ROIs. We found a significant interaction between condition, hemisphere, and group in the inhibition task ($F_{1,35}$=5.91, p=0.02). Post-hoc t-tests showed that this interaction was not due to differences between groups, but rather it was driven by higher activations in the left hemisphere in the deaf group during the congruent condition (t_{21}=2.32, p=0.03) (Figure S7).

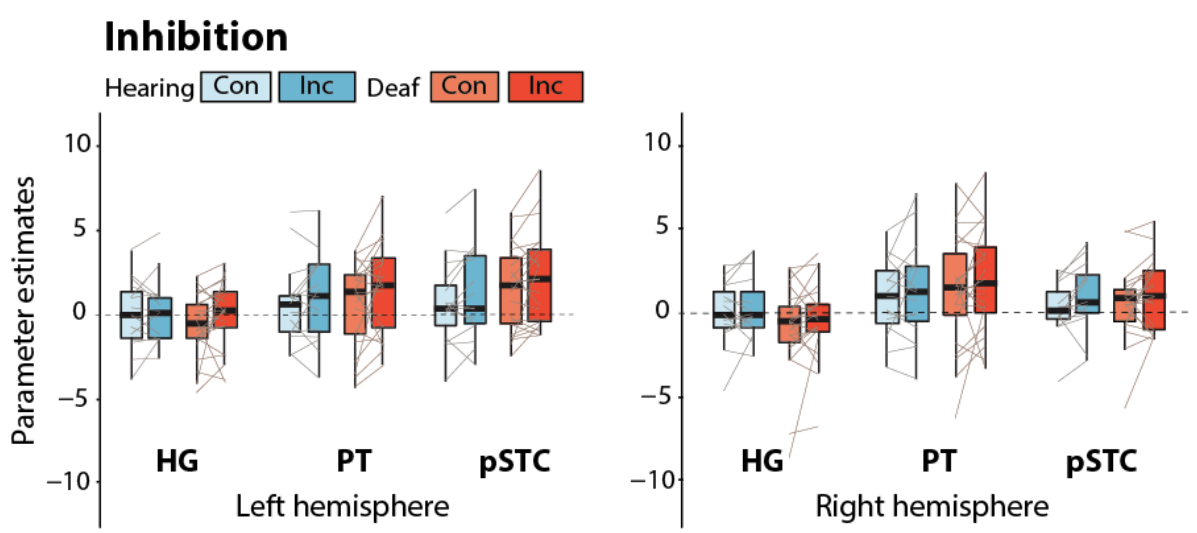


Figure 10. Temporal ROI analysis on inhibition. The neural activity in the temporal regions. Con=congruent, Inc=incongruent. HG=Heschl's gyrus, PT=the planum temporale, pSTC=the posterior superior temporal cortex.

Discussion

Here we investigated how early sensory and language experience impact the organisation of executive processing in the brain. We found that as a consequence of deafness, primary and secondary auditory areas are recruited during switching. Behavioural performance in this task correlated with activity in auditory areas and was modulated by language proficiency. Recruitment of auditory areas during switching correlated with the degree of deafness, more significantly in Heschl's gyrus, which contains the primary auditory cortex. These results suggest that early absence of auditory inputs results in a functional shift in regions typically involved in auditory processing — in the absence of auditory inputs, these regions adopt a role in specific components of executive processing with measurable consequences on the individual's behaviour. Recruitment of auditory regions was not observed in all EF tasks, indicating the absence of a common role in cognitive control in the deaf population. In the planning task, deaf individuals with the highest language scores also recruited secondary auditory regions. This suggests differences in the use of language to aid EF depending on early language experience and later proficiency, highlighting that superior temporal cortices have shared or overlapping roles in language and executive processing in deaf individuals (Cardin et al., 2020b).

Overall, we show executive processing in temporal regions typically considered to be auditory processing regions, suggesting that the involvement of regions in the adult brain for sensory or cognitive processing can be influenced by perceptual experience.

The auditory cortex of deaf individuals is recruited during task switching

To study the effects of early deafness on cortical reorganisation and executive processing, we mapped neural activity in a range of EF tasks: switching, working memory, planning, and inhibition. This design allowed us to thoroughly examine the role of auditory regions in components of executive function that are shared or unique across tasks. The HEF condition in all tasks recruited frontoparietal areas typically involved in EF and cognitive control. However, only switching resulted in significant activations in temporal auditory regions in the deaf group. This funding demonstrates that the deaf auditory cortex serves only a specific subcomponent of executive functioning during switching. If there were a general

role in cognitive control for these brain regions, similar activations would have been seen across all tasks.

Switching was also the only task where we found differences in accuracy between groups, where on average, performance in the group of deaf individuals was significantly lower. Accuracy in the switching task in the deaf group was linked to language proficiency, highlighting that poorer performance is not a consequence of crossmodal plasticity or deafness *per se*, but instead related to early language deprivation and consequent language delay (see below).

During the LEF and HEF conditions of the switching task, the deaf group activated temporal and frontoparietal regions more strongly than the hearing group. However, only in temporal areas did we find an interaction between group and condition and a correlation with behavioural performance. In the deaf group, the neural switch cost ($BOLD_{switch}$–$BOLD_{stay}$), correlated positively with the behavioural RT switch cost in left HG, right pSTC, and right PT. This direct relationship between behavioural outcomes and activity in reorganised cortical areas provides robust evidence of the functional and behavioural importance of the observed crossmodal plasticity. This relationship between higher neural activity and poorer behavioural performance indicates effortful processing, as has been previously observed in other cognitive tasks with different levels of complexity (Just et al., 1996; Cazalis et al., 2003). This same correlation was not found in the group of hearing individuals — instead, we found significant correlations in the opposite direction both for RT and accuracy, highlighting that these regions have different functional roles and consequences for performance in hearing and deaf individuals.

Switching requires cognitive flexibility and shifting between different sets of rules (Gurd et al., 2002; Rushworth et al., 2002). *Shifting* is considered one of the core components of executive control. It is defined as the ability to flexibly shift “back and forth between multiple tasks, operations, or mental sets” (Miyake et al., 2000). *Shifting* is also important in working memory tasks (2-back WM, visuospatial delayed recognition) that resulted in the recruitment of posterior superior temporal regions in deaf individuals. In the present study, the working memory task did not significantly recruit pSTC; we only observed moderate recruitment of the right PT, the magnitude of which was significantly smaller than that of the switching task

or previous WM studies (Ding et al. 2015; Cardin et al., 2018). The WM task we used in this study requires updating of information and incremental storage, but no shifting between targets or internal representations of stimuli. Together, these results suggest that previous WM effects in superior temporal regions are not necessarily linked to storage, updating or control, but are more likely linked to shifting between tasks or mental states.

A possible physiological mechanism supporting this change of function in the auditory cortex can be provided through its anatomical proximity to the parietal lobe, in particular the temporoparietal junction (TPJ), and to other middle and posterior temporal regions (Shiell et al., 2016; Cardin et al., 2020b). Right TPJ is a multisensory associative region involved in reorientation of attention to task-relevant information, such as contextual cues or target stimuli (Corbetta and Shulman, 2002; Geng and Mangun, 2011; Geng and Vossel, 2013; Larson and Lee, 2013, 2014; Tei et al., 2017). The right posterior temporal cortex also seems to have a role in attention in both deaf and hearing individuals (Seymour et al., 2017). Furthermore, portions of the middle temporal gyrus have been shown to be involved in task switching (Lemire-Rodger et al., 2019) and to encode task-set representations (Qiao et al., 2017). The anatomical location and the functional role of TPJ and other middle and posterior temporal regions suggest that, in the absence of auditory inputs throughout development, the computations performed by other temporo-parietal regions could be extended to adjacent auditory cortices (Shiell et al., 2016; Cardin et al., 2020b). However, the functional profile of these temporo-parietal areas, and in particular the link to behaviour, is the opposite to what we observed here — stronger optical imaging activations in the posterior temporal cortex were linked to faster reaction times in an attention task (Seymour et al., 2017) and higher activity in TPJ was associated with fewer errors during switching (Larson and Lee, 2013, 2014). In “auditory” temporal areas of the deaf brain, we observe the opposite pattern — higher activations in the switching condition are linked to slower responses and a larger switch cost. Thus, it is likely that the role of deaf “auditory” regions is different from that of adjacent temporo-parietal cortices.

Another possibility is that the recruitment of “auditory” temporal regions for switching observed in deaf adults reflects vestigial functional organisation present in early stages of development. Research on hearing children has found activations in bilateral occipital and superior temporal cortices during task switching (Engelhardt et al., 2019), with a similar

anatomical distribution to the one we find here. Our findings in deaf individuals suggest that executive processing in temporal cortices could be "displaced" by persistent auditory inputs which, as the individual develops, may require more refined processing or demanding computations. Thus, an alternative view is that regions considered to be "sensory" have mixed functions in infants and become more specialised in adults, following different developmental pathways influenced by environmental sensory experience: the temporal regions of hearing individuals become progressively more specialised for sound processing, whereas, in deaf adults, they are more specialised for subcomponents of executive processing.

Several studies of crossmodal plasticity propose a preservation of function in auditory areas, where these regions maintain their original computation but adapt to respond to a different sensory input (Lomber et al., 2010; Cardin et al., 2013; Bola et al., 2017; Benetti et al., 2017, 2021). Other studies have suggested that sensory-deprived auditory regions are involved in higher-order cognitive functions, suggesting a functional change (see for a review Cardin et al., 2020b). Taking into account different mechanisms that can support all these findings (Cardin et al., 2020b), as well as considering different developmental trajectories can contribute to more dynamic accounts of plasticity that depart from the dichotomy of preservation or change of function. This could include considering our choice of frame of reference, as "change" or "preservation" is usually defined with the developed neurotypical adult brain as the normative or reference comparison point. With the adult brain of hearing individuals as reference, our findings from the adult deaf brain can be seen as a change or shift towards cognitive processing, but perhaps there is preservation of function if we compare them to the early function of those regions in the developing brain.

Differences in reorganisation in primary and secondary auditory cortices

Our results show activations in all tested superior temporal areas during the switching task. This included Heschl's gyrus (HG), and specifically the Area Te1.0, which likely contains the human primary auditory cortex (PAC) (Morosan et al., 2001; Hackett, 2011; Dick et al., 2012). While crossmodal plasticity has been consistently found in higher-order auditory areas,), results from the primary auditory cortex are less consistent (see for a review Kral, 2007;

Butler and Lomber, 2013; Cardin et al., 2020b). Using fMRI, somatosensory stimulation has been shown to strongly recruit primary auditory areas in deaf individuals (Karns et al., 2012), but activations elicited by visual tasks are generally modest or absent, and in many cases, differences between deaf and hearing groups are driven by deactivations in the hearing group (Karns et al., 2012; Scott et al., 2014; Cardin et al., 2016; Retter et al., 2019). Here we found not only differences between groups, but significantly higher activations in the HEF condition and a correlation with behavioural performance, highlighting the relevance of this plasticity. These results show that crossmodal plasticity and a functional shift towards cognition can indeed occur in primary auditory regions. The only other fMRI study showing a behavioural link between activity in primary auditory areas and behaviour is that of Karns et al. (2012), where the authors found that the intensity of a double-flash visual illusion, elicited by concurrent somatosensory stimulation, correlated with activity in rostrocaudal HG (Area Te1.2). Together, these findings suggest that passive visual stimulation is not enough for activation of HG, but needs additional multisensory stimulation or executive demands, such as in the switching task. There were also notable differences between the patterns of activity observed in HG and secondary regions such as the planum temporale (PT) and pSTC. Activations during the switching condition were indeed of a smaller magnitude in HG than in the PT and pSTC. In addition, while there was an overall positive correlation between the degree of deafness and neural switch cost, this effect was only significant in HG. In the inhibition task, activations in the deaf group were higher in the PT and pSTC than in HG (significant group x ROI interaction). In the planning task, contrary to what was observed in the PT and pSTC, there were no significant correlations with language in HG, nor a positive trend (in agreement with our previous study (Cardin et al., 2016), where we found no significant activation for sign language processing in HG). These differences between primary and secondary areas may arise in part because HG is the first cortical relay of auditory inputs and has stronger subcortical inputs from the thalamus (Kaas et al., 1999). As such, any remaining auditory inputs are likely to have a more prominent effect here than in secondary auditory areas. This explains the effect of the degree of deafness, suggesting that only in those individuals with the most profound degrees of deafness would crossmodal reorganization in HG be observed. The closer vicinity of the PT and pSTC to middle temporal and parietal regions could also be a factor in driving more reorganization in these areas than in HG.

Language proficiency modulates cognitive processing and neural reorganisation

One of our goals was to investigate how language experience influences cognitive processing and neural reorganisation. In our study, deaf individuals were significantly less accurate in the switching task, with switching cost correlating with language scores. These results indicate that differences in task switching performance are driven by language experience, and not by an absence of auditory inputs. As a group, deaf participants also had significantly longer reaction times in all tasks. This is the opposite of what is often found in studies of visual reactivity in deaf individuals (Nava et al. 2008; Pavani and Bottari, 2012), highlighting critical differences in performance between purely perceptual tasks, and those who weigh more strongly on executive demands. Differences in performance in EF tasks have been previously described in studies of EF in deaf children, and they have been found to be associated with language delay (Figueras et al., 2008; Marshall et al., 2015; Botting et al., 2017). Similar results have been found when parental reports were used as an assessment of EF, with early language access having a stronger impact on EF than early access to sound (Hall et al., 2017, 2018). Differences in EF are not typically found in studies of deaf native signers (e.g. Hauser et al., 2008; Marshall et al., 2015; Cardin et al., 2018), who achieve language development milestones at the same rate as hearing individuals learning a spoken language. The studies exploring the link between EF and language experience in deaf individuals have been conducted mostly in children. The present research demonstrates that the developmental dynamics of the relationship between these two factors are preserved later in life: the level of language proficiency of an adult deaf individual still influences their performance on EF tasks. This evidence emphasises the importance of language development as it can have long-lasting effects on executive processing throughout the lifespan.

Behaviourally, participants with better language scores were also faster in the control condition of the planning task, which involved simple mathematical problem solving (van den Heuvel et al., 2003). Solving arithmetic operations activates the language network (Andin et al., 2015) and mathematical skills have been associated with language proficiency in the general population (Abedi et al., 2003, 2005; Brown, 2005; Han, 2008) and deaf students (Kelly and Gaustad, 2007). Our study confirms this association and shows that the

relationships between language and mathematical skills, and language and planning, also manifest in the brain. In the deaf group, language proficiency was associated with both neural activity and behavioural performance during the execution of both conditions of the planning task. The fact that we see a positive association between the neural activity in the PT and pSTC and the language scores of deaf participants in both the HEF and LEF conditions, with no interactions between them, indicates that what we observe is an effect of language processing, rather than executive processing. Unlike during switching, deaf participants do not recruit the PT and pSTC during the HEF condition of the planning task. The correlation with language reflects a different type of function: the PT and pSTC are involved in linguistic processing in deaf individuals (Corina et al., 1992, 1999; Neville et al., 1997, 1998; Emmorey et al., 2002; 2011; MacSweeney et al., 2002; Capek et al., 2009; Emmorey and McCullough, 2009; Cardin et al., 2013, 2016; Twomey et al., 2017). Given that the participants with higher language scores recruited these temporal regions more, we believe that deaf participants with better language skills use linguistic strategies to solve the tasks. Planning has been linked to verbal mediation (self-referring speech) (Fernyhough and Fradley, 2005; Al-Namlah et al., 2006), which is essential during early childhood for "thinking through" problems (Vygotsky, 1962). Language provides a foundation for planning and solving simple mathematical problems, being the medium through which higher-order (if-then) rules are formulated and a key to recursive thought (Zelazo et al., 2003). Developmental gains in language skills, specifically the ability to formulate hierarchical rules, are directly implicated in the development of EF (Best and Miller, 2010). In deaf individuals, this gain is supported by a larger degree of involvement of the temporal cortices during the planning task.

In summary, we propose that timely development of a first language boosts the overall efficiency of executive processing, regardless of whether the EF task itself allows implementation of purely linguistic mechanisms. Hierarchical rules of the "if-then" type can also be implemented, in an automatic way, during switching. Language can provide the necessary "framework" for these rules to develop and be used in a dynamic task in the most efficient way. Although participants are not required to use linguistic strategies during switching, we speculate that those who have benefited from the efficiency associated with developing such frameworks can invest less cognitive and neural resources into solving this task.

Conclusion

Here we show that executive processing in the adult brain is influenced by early sensory and language experience. While frontoparietal networks are involved in EF in both deaf and hearing individuals, deaf individuals also recruit superior temporal regions that are usually considered “auditory”. This recruitment was specific for switching and correlated with switching cost, suggesting a role of temporal regions in a subcomponent of executive control. Plasticity is linked to the degree of deafness in the primary auditory cortex, but the degree of deafness did not predict performance. These results suggest that the absence of auditory inputs “frees” superior temporal regions to take on functions other than sensory processing. This could be either by preserving a function these areas performed early in childhood or by taking on new functions driven by influences from top-down projections from frontoparietal areas or adjacent temporal and parietal regions. Only developmental neuroscience studies in deaf and hearing children will allow us to dissociate between these possibilities.

We show that developmental language experience can lead to varying outcomes for cognitive functions in the adult. Language scores, independently of modality, predicted accuracy in the switching task and reaction times in the control condition of the planning task (simple mathematical operation). Our study offers an insight into the role of language in executive processing by demonstrating how language can provide mechanisms that aid and optimise EF processing.

Overall, results from this study suggest different responses in deaf “auditory” temporal areas for executive and language processing. We have previously observed these shared functions, describing an overlap between working memory and language processing in superior temporal areas of deaf adults (Cardin et al., 2020b). By understanding the developmental trajectories of these changes we can move towards a unified theory of crossmodal plasticity.

Methods

Participants

There were two groups of participants (Table 3):

A. 29 congenitally or early (before 3 years of age) severely-to-profoundly deaf individuals whose first language is British Sign Language (BSL) and/or English (Table S4). We recruited a larger number of deaf participants to reflect the language variability of the deaf population in the UK, as discussed in the "Language assessment" section. Datasets from three deaf participants were excluded from all analyses due to excessive motion in the scanner. One participant was excluded because the pure-tone average (PTA) in their best ear was less than 70dB. There were a total of 25 deaf participants included in the analysis of at least one EF task (see Table S5 in the supplementary materials for details on exclusion).

B. 20 hearing individuals who are native speakers of English with no knowledge of BSL.

All participants communicated with the researchers in their preferred language: either directly in BSL or English or through a BSL interpreter. All participants gave their written informed consent. All procedures followed the standards set by the Declaration of Helsinki and were approved by the ethics committee of the School of Psychology at the University of East Anglia (UEA) and the Norfolk and Norwich University Hospital (NNUH) Research and Development department.

Participants travelled to the University of East Anglia (UEA) in Norwich. They were recruited through public events, social media, and the participant databases of the UCL (University College London) Deafness, Cognition and Language Research Centre (DCAL), and the UEA School of Psychology. Participants were all right-handed (self-reported), had normal or corrected-to-normal vision, and no history of neurological conditions. All participants were compensated for their time, travel, and accommodation expenses.

The final sample consisted of 25 deaf and 20 hearing participants matched on age, gender, non-verbal intelligence, and visuospatial working memory span ($p>0.05$ for each parameter) (Table 3, Table S6).

Table 3. Demographics and pre-screening tests

	Age		Gender	WASI		Corsi	
	Mean (range)	**SD**		**Mean**	**SD**	**Mean**	**SD**
Full sample hearing N=20	37.50 (18-66)	16.85	15f/5m	58.65	5.98	5.40	1.1
Full sample deaf N=25	41.68 (19-66)	14.38	16f/9m	59.68	8.51	5.30	0.77
WM hearing N=19	38.47 (18-66)	16.72	14f/5m	59.13	5.83	5.47	1.08
WM deaf N=24	40.43 (19-66)	14.17	15f/9m	59.96	8.58	5.38	0.70
Planning hearing N=19	39.95 (18-66)	17.13	14f/5m	58.81	6.13	5.47	1.14
Planning deaf N=21	40.81 (19-63)	13.65	13f/8m	59.67	9.19	5.26	0.82
Switching hearing N=20	37.50 (18-66)	16.85	15f/5m	58.65	5.98	5.40	1.1
Switching deaf N=23	39.27 (19-63)	13.33	14f/9m	59.87	8.76	5.91	0.71
Inhibition hearing N=15	40.33 (18-66)	17.09	12f/3m	59.25	6.5	5.46	1.25
Inhibition deaf N=22	40.59 (19-66)	14.87	14f/8m	60.05	8.84	5.43	0.70

Participants had to be excluded from the analyses of separate tasks. The reasons for exclusion are described in Table S5. Three hearing participants did not complete the nonverbal IQ assessment (WASI; Wechsler, 1999) and two of these participants also did not complete the visuospatial working memory Corsi task (Corsi, 1972).

General procedure

Each participant took part in a behavioural session and a scanning session. The sessions took place on the same or different days.

The behavioural session consisted of:

a) Standardised nonverbal IQ and working memory tests. The Block Design subtest of the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler 1999; Table 3) and a computerised version of the Corsi block-tapping task (Corsi, 1972) as implemented in PEBL software (http://pebl.sourceforge.net/).
b) Language tasks. Two tasks were administered to assess language proficiency in English and BSL in the group of deaf participants (see the "Language assessment" section below).
c) Pre-scanning training. The EF tasks used during the scanning sessions (see below) were explained to the participants in their preferred language (English or BSL). The training session ensured that participants were comfortable with the tasks and that their accuracy was above 75%.
d) Audiogram. Pure-tone averages (PTAs) were used to measure the degree of deafness in the group of deaf participants. Copies of audiograms were provided by the participants from their audiology clinics or, in case these were not available, collected at the time of testing using an R17 screening portable audiometer (Resonance,http://www.resonance-audiology.com/en/r17a-screening-audiometer/). Data from one participant who self-reported as severely deaf were excluded because they could understand spoken English without relying on lipreading, and their PTA threshold was less than 70dB. All remaining participants had a mean PTA greater than 75dB averaged across the speech frequency range (0.5, 1, 2kHz) in both ears (mean=93.66±7.79dB; range: 78.33-102.5dB). Four participants did not provide their audiograms but they were all congenitally severely or profoundly deaf and communicated with the researchers using BSL or relying on lipreading.

During the scanning session, fMRI data were acquired while participants performed four visual tasks tapping into different EF: working memory, planning, switching, and inhibition (see details below). The order of the tasks was counterbalanced across participants.

Language assessment

One of our aims was to investigate the relationship between language, EF, and neural reorganisation in the deaf group, independently of the modality of the preferred language of the individual (signed or spoken). To capture the variability in language proficiency in the British deaf population, we recruited a larger group of deaf participants with different language backgrounds (see Table S4 for details) and measured their language proficiency in English and BSL.

To assess the language proficiency of deaf participants we used grammaticality judgement tests measuring language skills in English and BSL. The BSL Grammaticality Judgement task (BSGJT) is described in Cormier et al. (2012b), and the English Grammaticality Judgement task (EGJT) was designed based on examples from Linebarger et al. (1983). The BSGJT and the EGJT use a single method of assessing grammaticality judgements of different syntactic structures in English and BSL. Grammaticality judgement tests have been used in deaf participants before (Boudreault and Mayberry, 2006; Cormier et al., 2012b), have proved to be efficient in detecting differences in language proficiency among participants with varying ages of acquisition (Cormier et al., 2012b) and thus can reflect the heterogeneity of language backgrounds seen in deaf communities.

During the same session, we also collected data from deaf signers on a BSL Sentence Reproduction Test (Cormier et al., 2012a) and from all participants on the Vernon-Warden Reading Comprehension Test Revised (1996). The results will be reported in a different manuscript. Deaf participants were tested either in both BSL and English tests if they knew both languages, or only in the English tests if they did not know BSL. Hearing participants were only tested in the English tests (for control purposes).

fMRI EF tasks

Working memory. We used a visuospatial working memory task (Fedorenko et al., 2011, 2013; Blank et al., 2014) (Figure 1), which was contrasted with a perceptual control task. All trials started with a visual cue (1500 ms) that indicated which task participants should perform. The cue was followed by a 3×4 grid. Randomly generated locations were sequentially highlighted two at a time for one second for a total of eight locations on the grid. In the working memory condition (HEF), participants indicated their cumulative memory for these locations by choosing between two grids in a two-alternative, forced-choice

paradigm via a button press. The response grids were displayed until the participant responded or for a maximum of 3750 ms. In the control condition (LEF), participants indicated whether a blue square was present in any of the grids, ignoring the configuration of the highlighted squares. Trials were separated by an inter-trial interval (ITI) with duration jittered between 2000-3500 ms. Each experimental run had 30 working memory trials and 30 control trials.

Planning. We used a computer version of the classic Tower of London task (Morris et al., 1993; van den Heuvel et al., 2003, Kaller et al., 2012; Figure 1). In each trial, two configurations of coloured beads placed on three vertical rods appeared on a grey screen, with the tallest rod containing up to three beads, the middle rod containing up to two beads, and the shortest rod containing up to one bead. In the Tower of London condition (HEF), participants had to determine the minimum number of moves needed to transform the starting configuration into the goal configuration following two rules: 1) only one bead can be moved at a time; 2) a bead cannot be moved when another bead is on top. There were four levels of complexity, depending on the number of steps required (2, 3, 4, and 5 moves). In the control condition (LEF), participants were asked to count the number of yellow and blue beads in both displays. For both conditions, two numbers were displayed at the bottom of the screen: one was the correct response and the other was incorrect by +1 or -1. Participants answered with their left hand when they chose the number that was on the left side of the screen, and with their right hand when their choice was on the right. The maximum display time for each stimulus was 30 seconds. The duration of the ITI was jittered between 2000-3500ms. There were 30 trials in the Tower of London condition and 30 trials in the control condition.

Switching. In this task, participants were asked to respond to the shape of geometric objects, i.e. a rectangle and a triangle (Rubinstein et al., 2001; Rushworth et al., 2002; Monsell, 2003; Liston et al., 2006; Figure 1). At the beginning of the run, participants were instructed to press a key with their left hand when they saw a rectangle and with their right hand when they saw a triangle. Each block started with a cue indicating that the task was to either keep the rule they used in the previous block ("stay" trials; LEF) or to switch it ("switch" trials; HEF). In the switch trials, participants had to apply an opposite mapping between the shape and the response hand. One block included the presentation of the instruction cue (200ms), a fixation cross (500 ms), and two to five trials of the task. Each trial consisted of up to 1500ms display of the geometrical shapes followed by feedback (500ms).

There were a total of 230 trials in 80 blocks of either the LEF (40) or HEF (40) condition. Only the first trial of the switch block was analysed in the HEF condition (see below).

Inhibition. To study inhibitory control, we used Kelly and Milham's (2016) version of the classic Simon task (https://exhibits.stanford.edu/data/catalog/zs514nn4996; Liu et al., 2004; Aron, 2007). The stimuli (squares) appeared on the left or the right side of the fixation cross. The colour of the squares was the relevant aspect of the stimuli, whereas their position was irrelevant for the task. Participants were instructed to respond to the red square with the left hand and the green square with the right hand. In the congruent condition (LEF), the button press response was spatially congruent with the location of the stimuli (e.g. the right-hand response for a square appearing on the right side of the screen) (Figure 1). In the incongruent condition (HEF), the correct answer was in the opposite location in respect to the stimulus (e.g. the left-hand response for a square appearing on the right side of the screen). Half of the trials were congruent, and half were incongruent. Each stimulus was displayed for 700 ms, with a response window of up to 1500 ms. The ITI was 2500ms for most trials. There were 20 blank intervals of 7.5 seconds, two intervals of 12.5 seconds, and one interval of 30 seconds. Participants completed 1 or 2 runs of this task, each consisting of a maximum of 200 trials.

Behavioural performance analysis on the EF tasks

Averaged accuracy (%correct) and reaction time (RT) were calculated. In the switching task, the switch cost was calculated as the difference in the percent of errors (%errors) or RT between the first switch trial of a switch block and all stay trials. In the inhibition task, the Simon effect was calculated as the difference in %errors or RT between the incongruent and congruent trials. We used %errors instead of %correct for switch costs and Simon effects so that higher numbers indicated larger costs or effects.

Differences between groups on accuracy or RT were explored with repeated-measures ANOVAs with between-subjects factor group (hearing, deaf) and within-subjects factor condition (LEF, HEF). The differences between the switch costs and Simon effects were tested with ANCOVAs with the switch cost or the Simon effect as a dependent variable and a fixed factor group (hearing, deaf).

To explore the effect of language proficiency on behavioural performance in the deaf group, language z-scores were included as covariates in separate ANCOVAs.

Image acquisition

Images were acquired at the Norfolk and Norwich University Hospital (NNUH) in Norwich, UK, using a 3 Tesla wide bore GE 750W MRI scanner and a 64-channel head coil. The researchers communicated with the deaf participants directly or with the help of a BSL interpreter using a close circuit camera, or in English by displaying messages on the screen. An intercom was used for communication with hearing participants. All volunteers were given ear protectors. Stimuli were presented with the use of the Psychopy software (Peirce, 2007; https://psychopy.org) through a laptop (MacBook Pro, Retina, 15-inch, Mid 2015). All stimuli were projected by an AVOTEC's Silent Vision projector (https://www.avotecinc.com/high-resolution-projector) onto a screen located at the back of the magnet's bore. Participants watched the screen through a mirror mounted on the head coil. Button responses were recorded via fORP (Fiber Optic Response Pads) button boxes (https://www.crsltd.com/tools-for-functional-imaging/mr-safe-response-devices/forp/).

Functional imaging data were acquired using a gradient-recalled echo (GRE) EPI sequence (50 slices, TR=3,000 ms, TE=50ms, FOV=192 ×192 mm, 2mm slice thickness, distance factor 50%) with an in-plane resolution of 3×3mm. The protocol included six functional scans: 1 resting state scan (will be reported in a different manuscript) and five task-based fMRI scans (working memory: 11 minutes, 220 volumes; planning: 11.5 minutes, 230 volumes; switching: 10.5 minutes, 210 volumes; inhibition: two runs of 10 minutes, 200 volumes each). Due to time constraints, some participants did not complete all functional scans (Table S5). An anatomical T1-weighted scan (IR-FSPGR, TI=400ms, 1mm slice thickness) with an in-plane resolution of 1×1mm was acquired during the session.

Raw B0 field map data were acquired using a 2D multi-echo GRE sequence with the following parameters: TR=700 ms, TE=4.4 and 6.9ms, flip angle=50°, matrix size=128×128, FOV=240 mm×240mm, number of slices=59, thickness=2.5mm, and gap=2.5 mm. Real and imaginary images were reconstructed for each TE to permit calculation of B0 field maps in Hz (Jezzard and Balabam, 1995; Fessler et al., 2005; Funai et al., 2008).

fMRI preprocessing

fMRI data were analysed using MATLAB (MathWorks, MA, USA) and Statistical Parametric Mapping software (SPM12; Wellcome Trust Centre for Neuroimaging, London, UK). The anatomical scans were segmented into different tissue classes: grey matter, white matter,

and cerebrospinal fluid. Skull-stripped anatomical images were created by combining the segmented images using the Image Calculation function in SPM (ImCalc, http://tools.robjellis.net). The expression used was: [(i1. *(i2+i3+i4))>threshold], where i1 was the bias-corrected anatomical scan and i2, i3 and i4 were the tissue images (grey matter, white matter, and cerebrospinal fluid, respectively). The threshold was adjusted between 0.5 and 0.9 to achieve adequate brain extraction for each participant. Each participant's skull-stripped image was normalised to the standard MNI space (Montreal Neurological Institute) and the deformation field obtained during this step was used for normalisation of the functional scans. Susceptibility distortions in the EPI images were estimated using a field map that was co-registered to the BOLD reference (Fessler et al., 2005, Funai et al., 2008). Images were realigned using the pre-calculated phase map, co-registered, slice-time corrected, normalised, and smoothed (using an 8mm FWHM Gaussian kernel). All functional scans were checked for motion and artefacts using the ART toolbox (https://www.nitrc.org/projects/artifact_detect).

fMRI first-level analysis

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

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

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

Planning. Tower of London (HEF) and control (LEF) conditions were included in the model as regressors of interest, with onsets at the beginning of each trial and duration set to the

trial-specific RT. Button responses were modelled separately for each hand as regressors of no interest.

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

Whole-brain second-level analysis

Beta values for each regressor of interest in each task were taken into separate second-level repeated measures ANOVAs as described in the results. Significantly active voxels at $p<0.05$ FWE-corrected peak- or cluster-level (peak $p<0.001$) are reported in the results section as x, y, and z coordinates in the standard MNI space.

Region of interest analysis

We conducted a region of interest (ROI) analysis to investigate differences between groups in executive processing and their relationship to behavioural variables. Identifying main effects and interactions between groups, conditions, and behaviour, across all voxels in the brain, requires a large number of comparisons. In order to acquire enough data to conduct this type of whole-brain analysis for four different tasks, we would need very long or multiple scanning sessions — this is not feasible when testing special populations, where many participants have to travel from different parts of the country. For that reason, we limited our statistical inferences to two predefined sets of ROIs: temporal auditory regions and frontoparietal areas.

Temporal ROIs definition

Three regions of the superior temporal cortex were included in this analysis: Heschl's gyrus (HG), the planum temporale (PT), and the posterior superior temporal cortex (pSTC) (Figure 6A).

HG and the PT were defined anatomically, using the FreeSurfer software package (https://surger.nmr.mgh.harvard.edu). Full descriptions of these procedures can be found in previous publications (Dale et al., 1999; Fischl and Dale, 2000; Fischl et al., 2001, 2002, 2004, Ségonne et al., 2004; Han et al., 2006; Jovicich et al., 2006). In short, each participant's bias-corrected anatomical scan was parcellated and segmented, and voxels with the HG label and the PT label were exported using SPM's ImCalc function (http://robjellis.net/tools/imcalc_documentation.pdf). Participant-specific ROIs were then normalised to the standard MNI space using the deformation field from the normalisation step of the participants' data pre-processing.

We specified pSTC based on findings from Cardin et al. (2018), where a visual working memory crossmodal plasticity effect is described in right and left pSTC in deaf individuals [left: -59 -37 10; right: 56 -28 -1]. For this study, right and left functional pSTC ROIs were defined from the data of Cardin et al. (2018) using the contrast [deaf (working memory > control task) > hearing (working memory > control task)] ($p<0.005$, uncorrected).

There was a partial overlap between left PT and left pSTC in 39 participants. The average overlap between these ROIs was 8.2 voxels (SD=6.86), with no significant difference between the groups (deaf: mean=9.92, SD=7.02; hearing: mean=6.05, SD=6.17). To ensure that the two ROIs were independent, common voxels were removed from left PT in a subject-specific manner. Removing the overlapping voxels did not qualitatively change the results.

Post-hoc ROI analysis of Te 1.0

Area Te 1.0 of HG was defined using the cytoarchitectonic maps generated by Tahmasebi et al. (2009), based on those produced by Morosan et al. (2001). Subject-specific cytoarchitectonic ROIs were specified by combining, separately for each hemisphere, voxels that were present both in the participant-specific FreeSurfer HG ROI and in the Te 1.0 map from Tahmasebi et al. (2009).

Frontoparietal ROIs definition

Frontoparietal ROIs were defined by extracting uniformity clusters from a meta-analysis map of 128 studies associated with the keyword "executive function" using neurosynth.org (Yarkoni et al., 2011). From the uniformity clusters, we created spherical, symmetrical, and bilateral ROIs using MarsBaR (MARSeille Boîte À Région d'Intérêt,

http://marsbar.sourceforge.net, Brett et al., 2002). The anatomical labels of the ROIs, the MNI coordinates, and their radius are shown in Figure S1. Areas of interest were dorsolateral prefrontal cortexes (DLPFC), frontal eye fields (FEF), pre-supplementary motor area (pre-SMA), the insula, and the superior parietal lobule (SPL). We set a 10-mm radius for the DLPFC, FEF, and SPL, an 8-mm radius for the insula, and a 7-mm radius for the pre-SMA to exclude voxels in neighbouring gyri.

Extraction of contrast values and statistical analysis

Parameter estimates were extracted from each ROI using MarsBaR 0.44 (http://marsbar.sourceforge.net; Brett et al., 2002). All the statistical analyses presented in the results section were conducted using JASP (https://jasp-stats.org). The data were entered into separate repeated-mixed measures ANOVAs for each task and set of ROIs. Factors in the ANOVAs included: the between-subjects factor group (hearing, deaf) and the within-subjects factors ROI (temporal: HG, PT, pSTC; frontoparietal: DLPFC, FEF, pre-SMA, insula, SPL), hemisphere (left, right), and condition (LEF, HEF). For the language analysis (deaf group only), we conducted separate repeated-measures ANOVAs for each task with factors ROI (temporal: HG, PT, pSTC; frontoparietal: DLPFC, FEF, pre-SMA, insula, SPL), hemisphere (left, right), and condition (LEF, HEF) and used language z-score as a covariate. In the switching task, the neural switch cost was calculated by subtracting the average neural activity in all stay trials ($BOLD_{stay}$) from the average activity in the first switch trials ($BOLD_{switch}$). This was then used to calculate correlation coefficients with relevant behavioural variables.

The Greenhouse-Geisser correction was applied when the assumption of sphericity was violated. Significant interactions and effects of interest were explored by conducting the Student's t-tests or calculating Pearson's correlation coefficients. Mann-Witney U-tests were used when the equal variance assumption was violated.

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Data sharing

Preprocessed data and statistical analyses can be found here: https://osf.io/uh2ap/.
Raw images will be shared after the conclusion of the grant. Please contact the researchers directly if you would like to access the raw data before its publication.

Supplementary materials

Figures

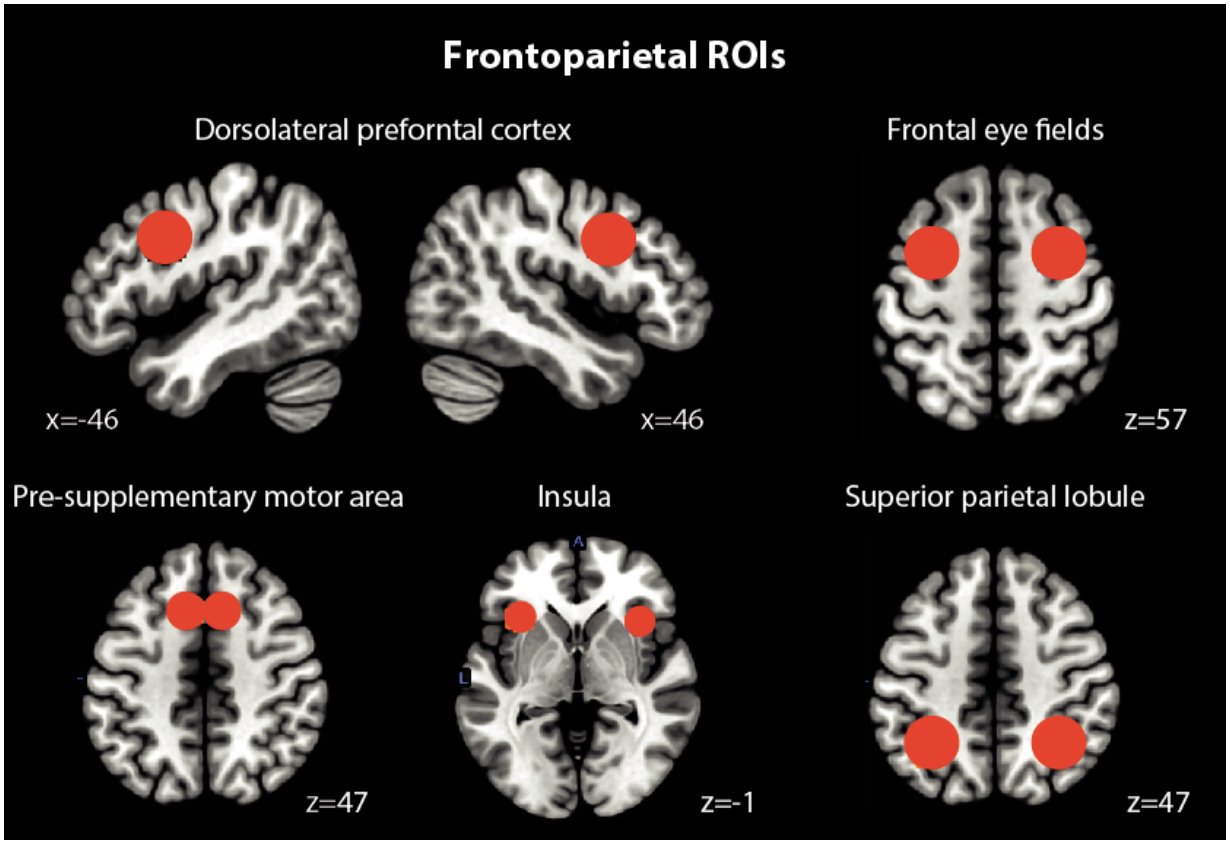

Figure S1. Frontoparietal spheric ROIs. Numbers in brackets indicated the central coordinates of the ROI: the dorsolateral prefrontal cortex (DLPFC) [left: -46 6 32; right: 46 8 32; radius 10mm]; frontal eye fields (FEF) [left: -29 0 57, right: 29 0 57; radius 10mm]; pre-supplementary motor area (pre-SMA) [left: -6 16 46, right: 6 16 46; radius 8mm]; the insula [left: -34 21 0, right: 36 19 -2; radius 7mm]; the superior parietal lobule (SPL) [left: -34 -55 46, right: 34 -55 46; radius 10mm].

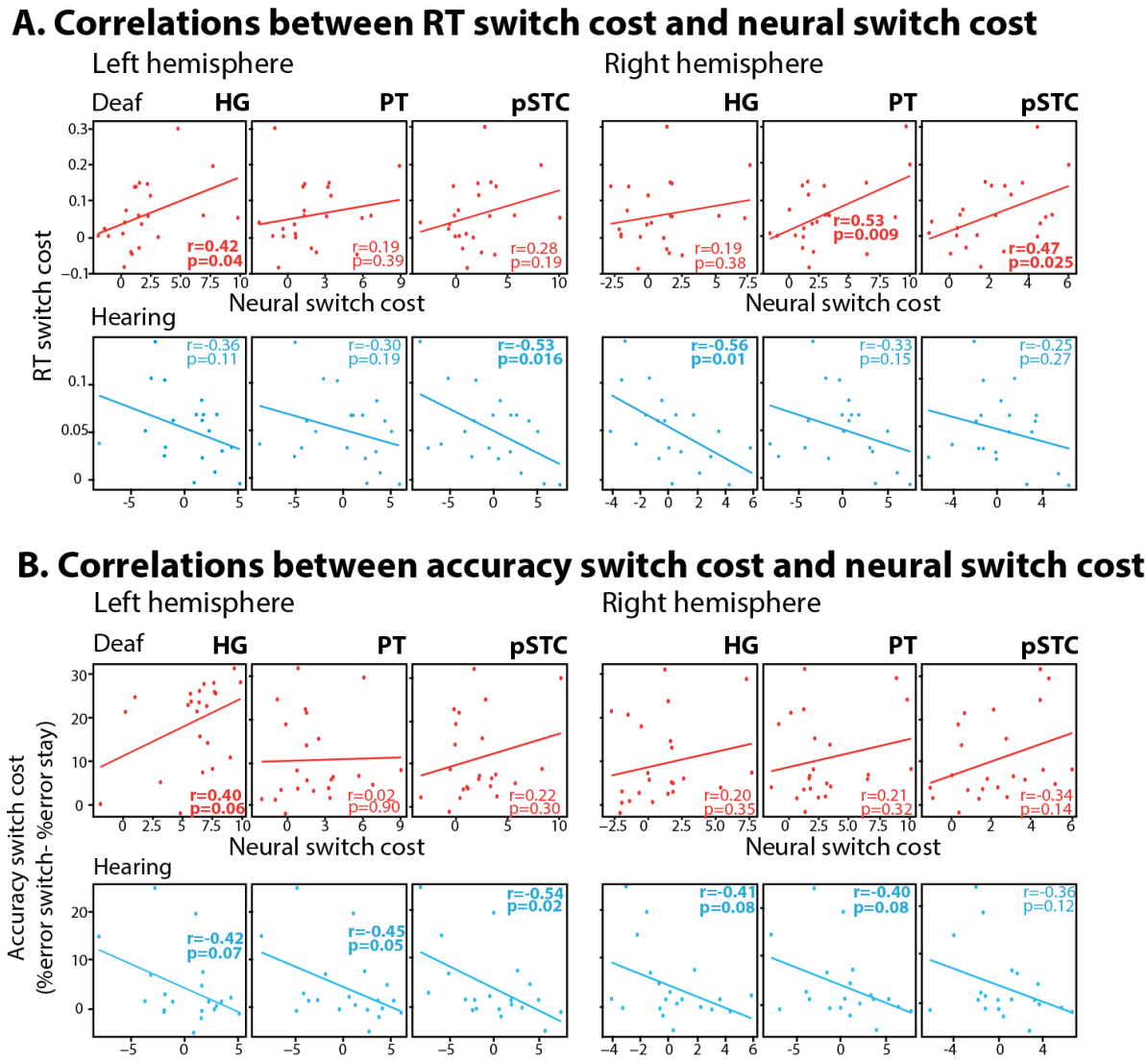

Figure S2. Correlations between neural and behavioural responses during switching. **A.** Correlations between neural switch cost and RT switch cost. **B.** Correlations between neural switch cost and %error for accuracy. HG=Heschl's gyrus, PT=the planum temporale, pSTC=the posterior superior temporal cortex.

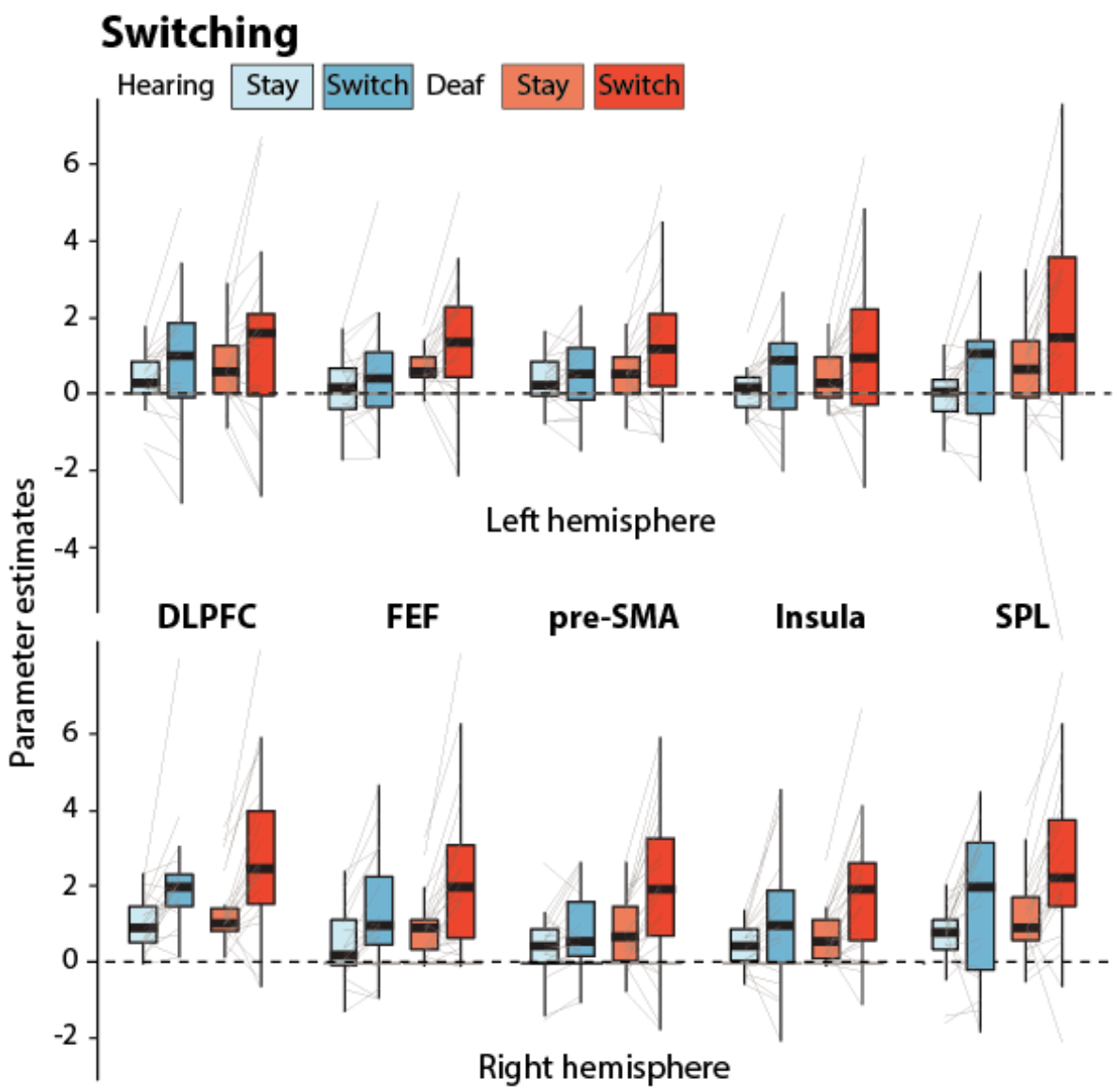

Figure S3. Frontoparietal ROI analysis on switching. Neural activity in the frontoparietal regions. DLPFC=the dorsolateral prefrontal cortex, FEF=frontal eye fields, pre-SMA=pre-supplementary motor area, SPL=the superior parietal lobule.

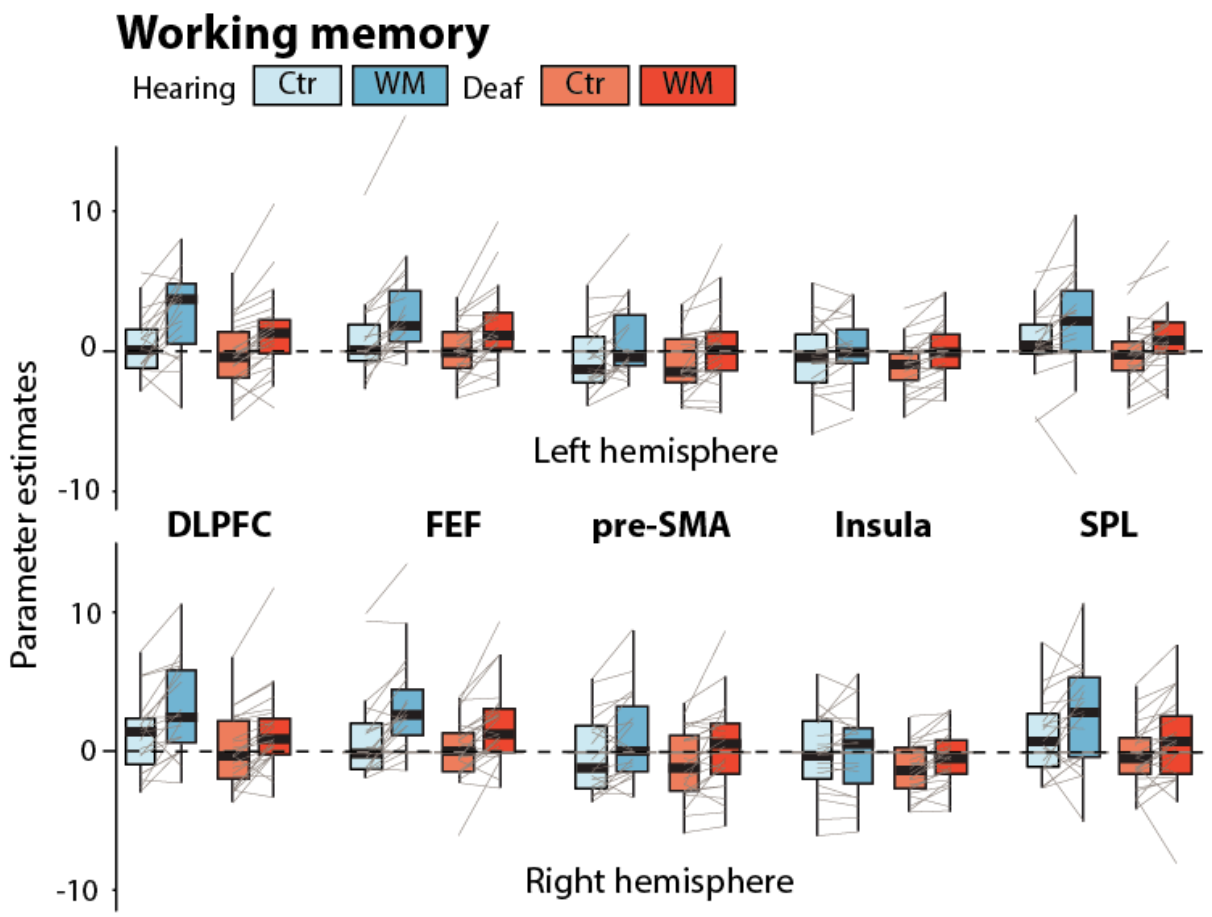

Figure S4. Frontoparietal ROI analysis on working memory. Neural activity in the frontoparietal regions. Ctr=control, WM=working memory. DLPFC=the dorsolateral prefrontal cortex, FEF=frontal eye fields, pre-SMA=pre-supplementary motor area, SPL=the superior parietal lobule.

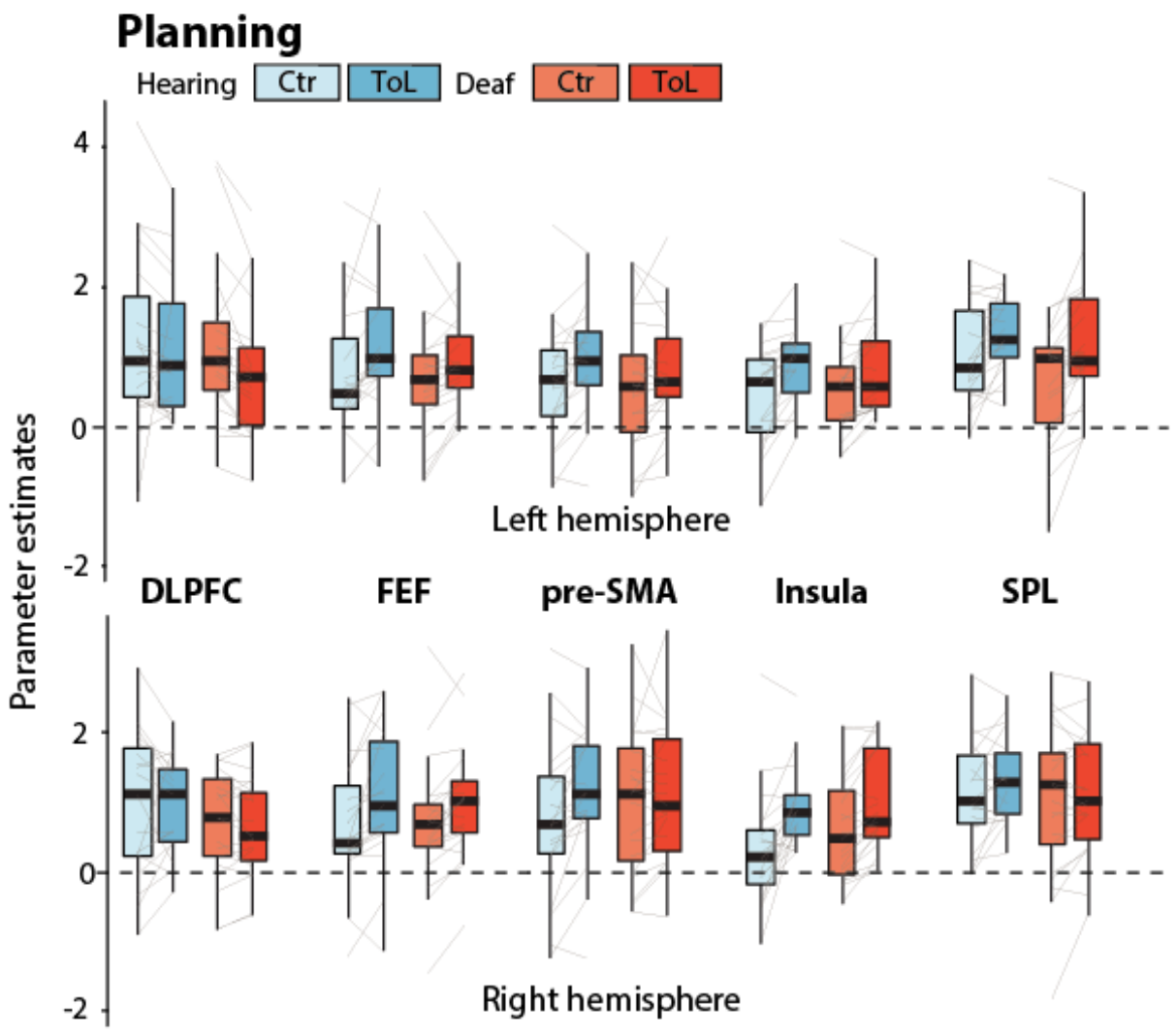

Figure S5. Frontoparietal ROI analysis on planning. Neural activity in the frontoparietal regions. Ctr=control, ToL=Tower of London. DLPFC=the dorsolateral prefrontal cortex, FEF=frontal eye fields, pre-SMA=pre-supplementary motor area, SPL=the superior parietal lobule.

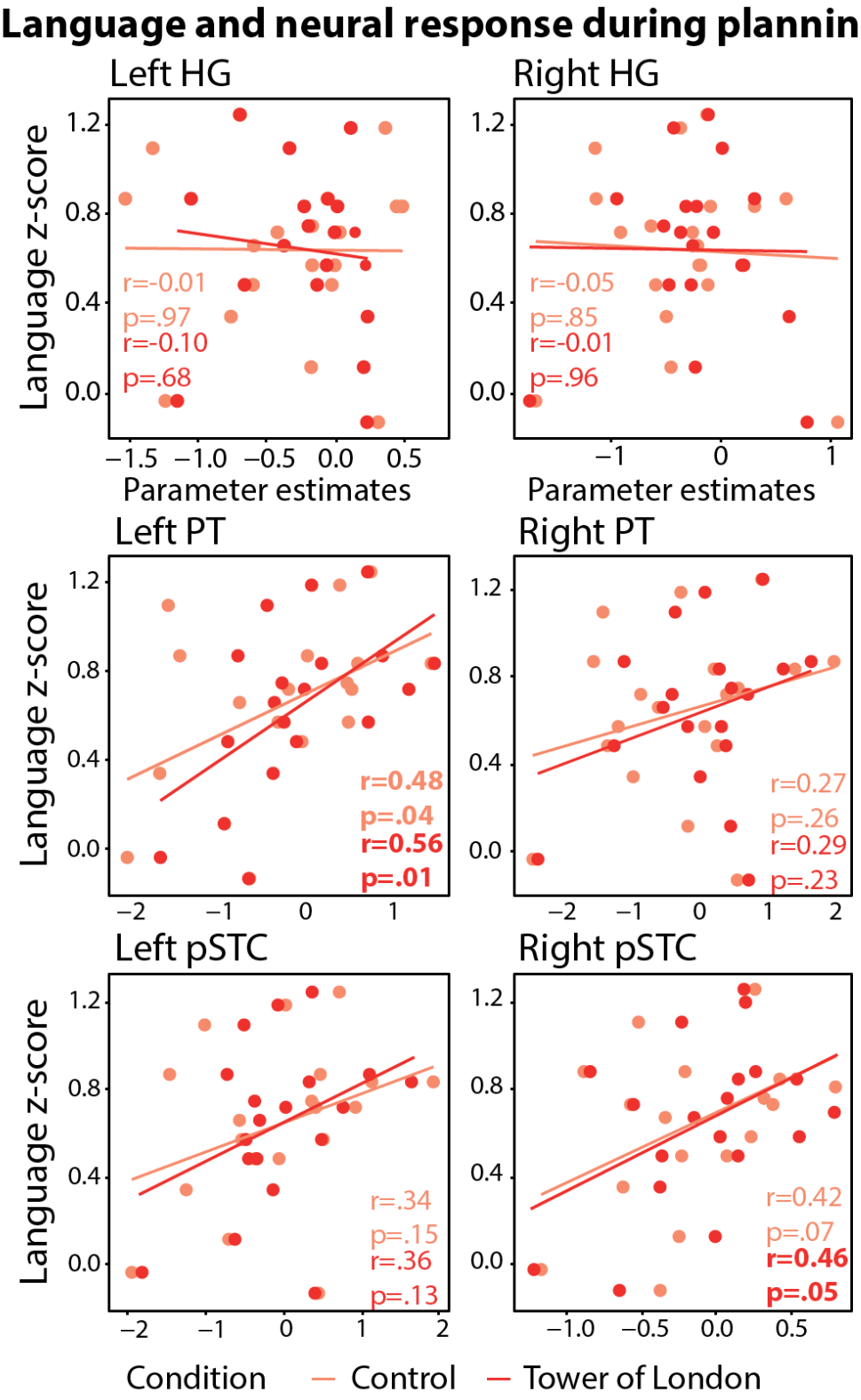

Figure S6. Correlations between language and neural response in the deaf group. HG=Heschl's gyrus, PT=the planum temporale, pSTC=the posterior superior temporal cortex.

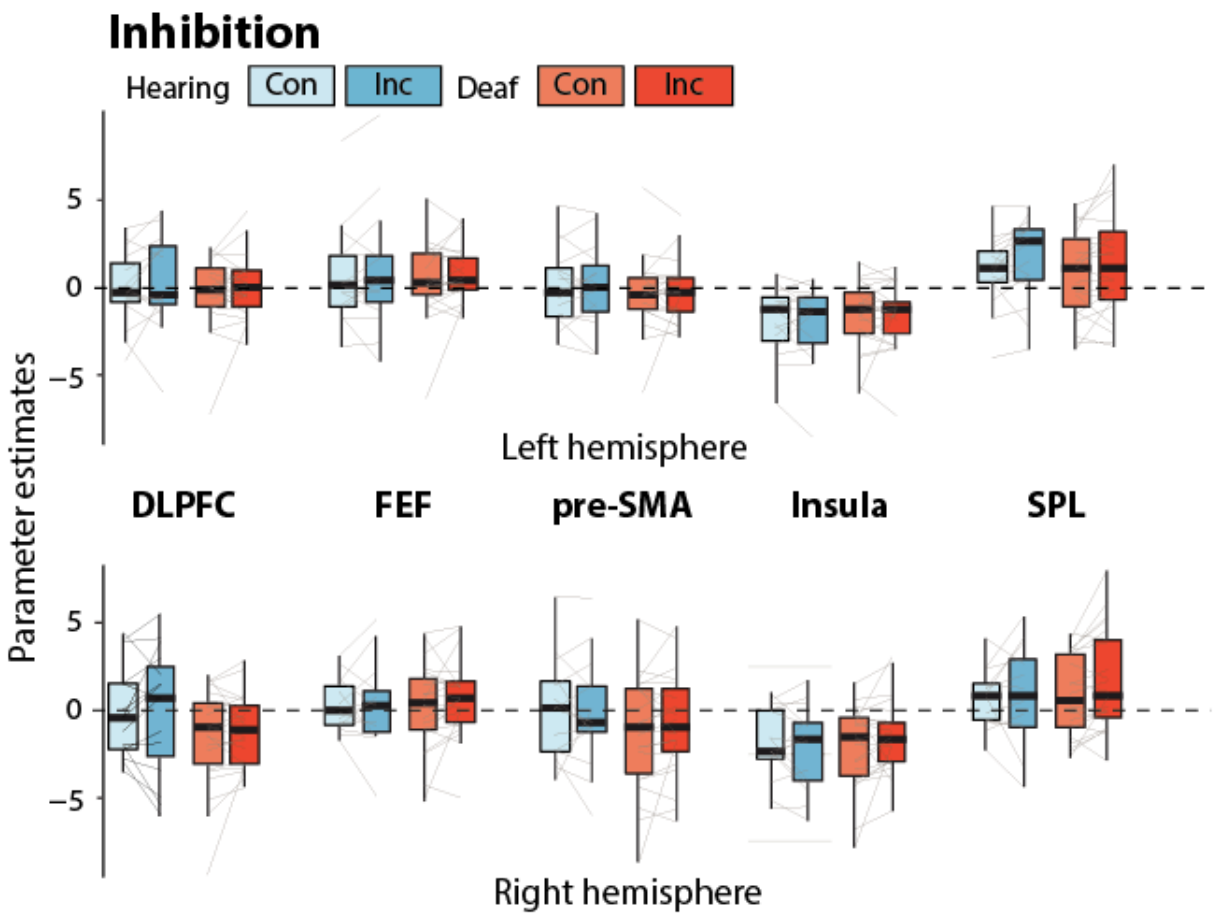

Figure S7. Frontoparietal ROI analysis on inhibition. Neural activity in the frontoparietal regions. Con=congruent, Inc=incongruent. DLPFC=the dorsolateral prefrontal cortex, FEF=frontal eye fields, pre-SMA=pre-supplementary motor area, SPL=the superior parietal lobule.

Tables

Table S1. Behavioural performance in the EF tasks

	WM		**Planning**		**Switching**		**Inhibition**	
	N hearing=19		*N* hearing=19		*N* hearing=20		*N* hearing=15	
	N deaf=24		*N* deaf=21		*N* deaf=23		*N* hearing=22	
	WM	**Ctr**	**ToL**	**Ctr**	**Switch**	**Stay**	**Incong.**	**Cong.**
	Accuracy (%correct)							
	M (SD)	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*
hearing	82.31	97.95	74.62	91.52	91.56	95.74	94.75	97.79
	(9.7)	(4.01)	(11.85)	(11.92)	(10.11)	(4.88)	(2.49)	(2.46)
deaf	83.57	97.55	76.51	94.18	82.56	93.16	94.19	96.97
	(9.76)	(3.16)	(10)	(11.26)	(13.71)	(5.81)	(4.31)	(2.6)
	Reaction time (correct responses only, seconds)							
	M (SD)	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*
hearing	1.48	0.68	7.07	2.7	0.56	0.51	0.49	0.46
	(0.4)	(0.13)	(1.92)	(0.47)	(0.1)	(0.07)	(0.08)	(0.07)
deaf	1.65	0.87	7.99	3.91	0.63	0.57	0.54	0.52
	(0.39)	(0.28)	(1.44)	(1.49)	(0.13)	(0.08)	(0.08)	(0.08)

Note. Average behavioural performance in all EF tasks for both groups. Incong.=incongruent; Cong.=congruent.

Table S2A. Language and behavioural performance in the deaf group

Accuracy		*df*	*F*	*p*
Working memory	Condition	1, 20	3.38	0.09
	Condition x language z-score	1, 20	3.08	0.1
	Language z-score	1, 20	0.27	0.61
Switching	Condition	1, 19	21.61	<0.001
	Condition x language z-score	**1, 19**	**4.82**	**0.04**
	Language z-score	1, 19	4.1	0.06
Planning	Condition	1, 17	1.21	0.29
	Condition x language z-score	1, 17	3.83	0.07
	Language z-score	1, 17	3.36	0.08
Inhibition	Condition	1, 18	0.69	0.42
	Condition x language z-score	1, 18	0.26	0.62
	Language z-score	1, 18	2.63	0.12
Reaction time		*df*	*F*	*p*
Working memory	Condition	1, 20	13.73	0.001
	Condition x language z-score	1, 20	1.37	0.26
	Language z-score	1, 20	0.03	0.6
Switching	Condition	1, 19	3.56	0.07
	Condition x language z-score	1, 19	0.32	0.58
	Language z-score	1, 19	3.08	0.1
Planning	Condition	1, 17	14.43	0.001
	Condition x language z-score	**1, 17**	**7.23**	**0.02**
	Language z-score	1, 17	2.37	0.14
Inhibition	Condition	1, 18	5.38	0.03
	Condition x language z-score	1, 18	0.09	0.76
	Language z-score	1, 18	0.39	0.54

Note. The table shows results of repeated-measures ANOVAs with condition (HEF, LEF) as a within-subjects factor and language z-score as a covariate. Bold letters indicate significant language effects.

Table S2B. Language, switch costs, and Simon effects in the deaf group

Switching	*df*	*F*	*p*
Switch cost (Accuracy)	**1, 19**	**4.82**	**0.04**
Switch cost (RT)	1, 19	0.28	0.61
Inhibition	*df*	*F*	*p*
Simon effect (Accuracy)	1, 18	0.26	0.62
Simon effect (RT)	1, 18	0.16	0.69

Note. The table shows results of ANCOVAs with switch costs or Simon effects as dependent variable and language z-score as a covariate in the deaf group. Bold letters indicate significant effects of language.

Table S3. Peak activation for the contrast [HEF > LEF] in both the groups for the working memory, planning, and switching tasks

Name		Working memory Peak voxels				Planning Peak voxels				Switching Peak voxels			
		z-score	*x*	*y*	*z*	*z-score*	*x*	*y*	*z*	*z-score*	*x*	*y*	*z*
Superior parietal lobule	L	7.11	-15	-67	53	6.98	-6	-61	59	6.37	-33	-52	56
	R	6.18	48	-58	35	6.86	42	-70	38	-	-	-	-
Supramarginal gyrus	L	-	-	-	-	6.59	-57	-40	47	-	-	-	-
	R	-	-	-	-	> 8	51	-46	50	5.82	60	-37	23
Angular gyrus	L	6.71	-36	-43	44	6.99	-51	-52	47	-	-	-	-
	R	6.82	33	-78	35	-	-	-	-	-	-	-	-
Pre-SMA	L	4.71	-6	17	44	6.49	-18	17	59	5.99	-24	-7	71
	R	5.04	42	20	44	-	-	-	-	6.04	51	5	41
Inferior frontal gyrus	L	7.51	-45	5	23	5.94	-45	41	-7	-	-	-	-
	R	6.79	51	8	23	-	-	-	-	-	-	-	-
Dorsolateral prefrontal cortex	L	4.82	-21	44	32	5.74	-42	26	38	-	-	-	-
	R	5.31	45	38	11	6.44	42	29	32	-	-	-	-
Fusiform gyrus	L	6.85	-51	-61	-4	-	-	-	-	-	-	-	-
	R	-	-	-	-	-	-	-	-	6.31	33	-58	-19
Frontal eye fields	L	6.85	-27	7	53	6.42	-6	32	23	-	-	-	-
	R	6.74	27	4	53	7.04	-0	29	41	-	-	-	-
Anterior prefrontal cortex	L	5.53	21	56	23	6.49	-36	53	8	-	-	-	-
	R	6.03	12	38	47	6.67	30	56	-1	-	-	-	-
Insula	L	-	-	-	-	6.46	-30	23	-7	5.56	-30	14	8
	R	-	-	-	-	-	-	-	-	5.7	39	2	5
Postcentral gyrus	L	-	-	-	-	-	-	-	-	-	-	-	-
	R	-	-	-	-	-	-	-	-	6.99	15	-94	-4
Extra-calcarine cortex	L	-	-	-	-	-	-	-	-	6.25	18	-85	-10
	R	7.46	18	-58	20	-	-	-	-	6.85	-15	-97	5
Precentral gyrus	L	-	-	-	-	-	-	-	-	6.86	-60	-19	23
	R	-	-	-	-	-	-	-	-	6	-48	-31	50
Anterior cingulate area	R	-	-	-	-	5.5	6	35	20	-	-	-	-

Note. All values are significant ($p<0.05$, FWE) at peak level. L=left, R=right.

Table S4. Deafness and language background of the deaf participants

ID	Onset of deafness	Cause of deafness	Native language	Preferred language	Other languages
1	0	Unknown	BSL	BSL	
2	0	Other	English	BSL	SASL
3	0	Genetic	BSL	BSL	
4	0	Genetic	English	English	
5	0	Genetic	BSL	BSL	
6	0	Genetic	BSL	BSL	
7	< 3 years old	Meningitis	Gesture or home sign, BSL	BSL	
8	0	Genetic	English	English	
9	0	Genetic	English	English	
10	0	Unknown	English	English	BSL
11	0	Genetic	BSL	BSL	ASL
12	0	Unknown	English	English	BSL
13	0	Mother had rubella	English	English	
14	0	Unknown	English	BSL	
15	0	Genetic	English	BSL	
16	0	Mother had rubella	English	English	
17	0	Genetic	English	English	
18	< 3 years old	Genetic	Auslan	Auslan	BSL, ASL
19	0	Genetic	English, BSL	English	
20	0	Genetic	English	BSL	
21	0	Mother had rubella	English	English	
22	< 3 years old	Genetic	BSL	BSL	
23	< 3 years old	Genetic	English	BSL	
24	0	Genetic	English	BSL	
25	0	Mother had infection	Gesture/home sign, BSL	BSL	

Note. All participants know English to some extent. ASL=American Sign Language, BSL=British Sign Language, SASL=South African Sign Language.

Table S5. List of participants included in each of the EF tasks

Group	ID	WM	Planning	Switching	Inhibition
Hearing	1	+	+	+	+
Hearing	2	- (performance)	+	+	- (not performed)
Hearing	3	+	+	+	- (not performed)
Hearing	4	+	+	+	- (not performed)
Hearing	5	+	+	+	+
Hearing	6	+	+	+	+
Hearing	7	+	+	+	- (performance)
Hearing	8	+	+	+	- (not performed)
Hearing	9	+	+	+	+
Hearing	10	+	+	+	+ (1 run)
Hearing	11	+	- (performance)	+	+
Hearing	12	+	+	+	+
Hearing	13	+	+	+	+
Hearing	14	+	+	+	+
Hearing	15	+	+	+	+
Hearing	16	+	+	+	+
Hearing	17	+	+	+	+
Hearing	18	+	+	+	+
Hearing	19	+	+	+	+
Hearing	20	+	+	+	+
Deaf	21	+	+	+	+
Deaf	22	+	- (not performed)	- (not performed)	+ (1 run)
Deaf	23	+	+	+	- (not performed)
Deaf	24	+	- (performance)	+	- (not performed)
Deaf	25	+	+	+	+ (1 run)
Deaf	26	+	+	+	+
Deaf	27	+	+	+	+
Deaf	28	+	+	+	+
Deaf	29	- (performance)	+	- (performance)	- (missing responses)
Deaf	30	+	- (movement)	+	+
Deaf	31	+	+	+	+ (1 run)
Deaf	32	+	+	+	+
Deaf	33	+	+	+	+
Deaf	34	+	+	+	+
Deaf	35	+	+	+	+
Deaf	36	+	+	+	+
Deaf	37	+	+	+	+
Deaf	38	+	+	+	+
Deaf	39	+	- (performance)	+	+ (1 run)
Deaf	40	+	+	+	+
Deaf	41	+	+	+	+ (1 run)
Deaf	42	+	+	+	+
Deaf	43	+	+	+	+
Deaf	44	+	+	+	+
Deaf	45	+	+	+	+

Note. "Performance" means the participant had a low (<55%) accuracy score in one of the conditions of interest.

Table S6. Between-group comparisons on demographics and pre-screening tests

	N	N	Age			Gender		WASI			Corsi		
	hearing	deaf	*df*	*t*	*p*	X^2	*p*	*df*	*t*	*p*	*df*	*t*	*p*
WM	19	24	1,41	0.61	0.55	0.6	0.44	1,38	0.34	0.74	1,39	-0.45	0.66
Planning	19	21	1,38	0.79	0.43	0.63	0.43	1,35	0.32	0.75	1,36	-0.45	0.65
Switching	20	23	1,41	0.60	0.55	0.97	0.32	1,38	-0.5	0.62	1,39	0.09	0.93
Inhibition	15	22	1,35	0.05	0.96	4.24	0.04	1,32	0.27	0.79	1,33	-0.09	0.92

Note. Some participants were excluded from the analyses of individual tasks. The reasons for exclusion are described in Table S5.

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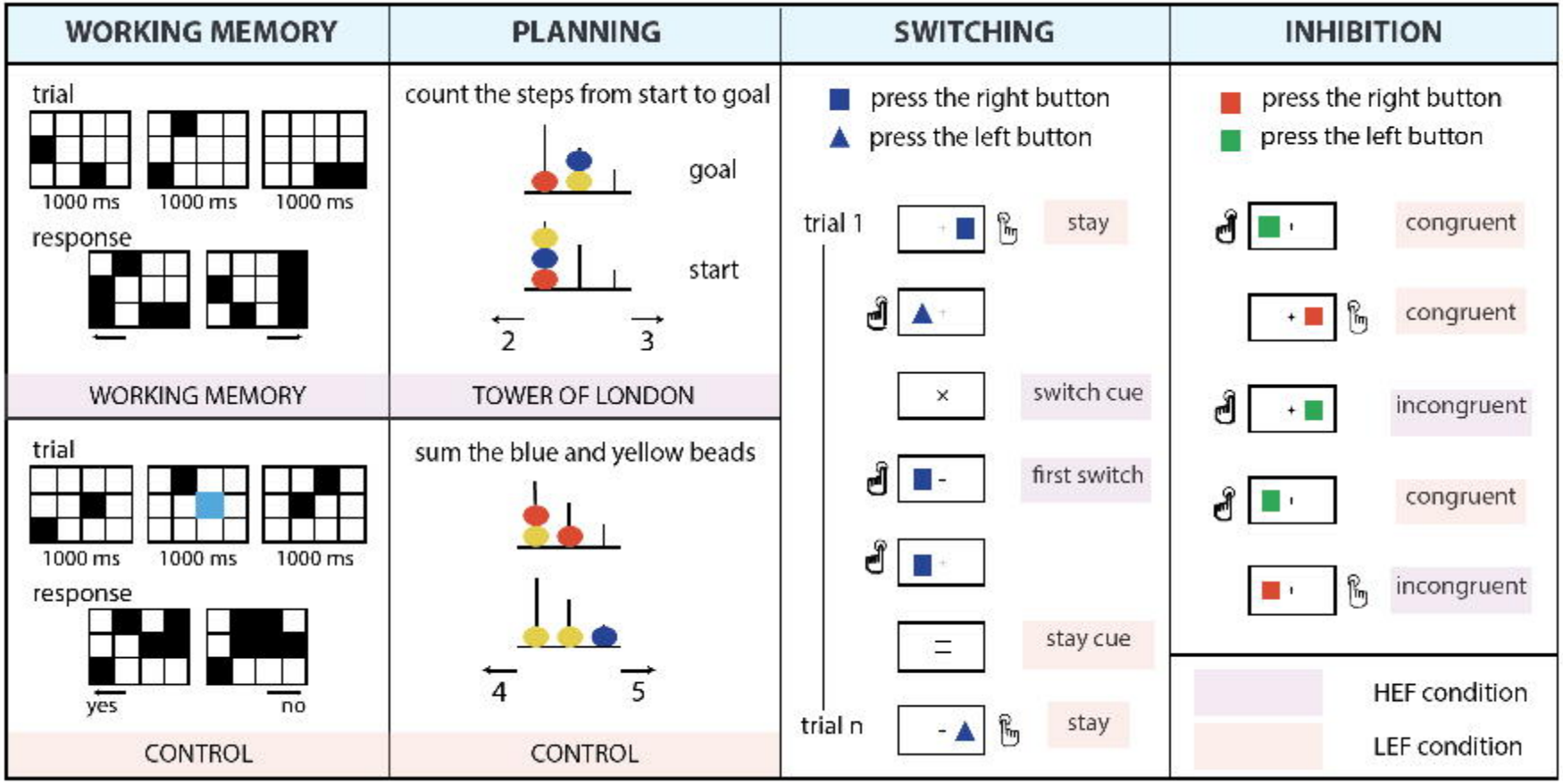
WORKING MEMORY
PLANNING
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trial
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WORKING MEMORY
count the steps from start to goal
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3
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CONTROL
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