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**Research Articles: Behavioral/Cognitive**

## **How auditory experience differentially influences the function of left and right superior temporal cortices**

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1 How auditory experience differentially influences the function of left and right superior  
2 temporal cortices

3

4 Abbreviated title: Functions of STC in deaf and hearing signers

5

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29 Abstract

30 To investigate how hearing status, sign language experience and task demands  
31 influence functional responses in the human superior temporal cortices (STC) we collected  
32 fMRI data from deaf and hearing participants (male and female), who either acquired sign  
33 language early or late in life. Our stimuli in all tasks were pictures of objects. We varied  
34 the linguistic and visuospatial processing demands in three different tasks that involved  
35 decisions about (1) the sublexical (phonological) structure of the British Sign Language  
36 (BSL) signs for the objects; (2) the semantic category of the objects; and (3) the physical  
37 features of the objects.

38 Neuroimaging data revealed that in participants who were deaf from birth, STC  
39 showed increased activation during visual processing tasks. Importantly, this differed  
40 across hemispheres. Right STC was consistently activated regardless of the task whereas  
41 left STC was sensitive to task demands. Significant activation was detected in the left STC  
42 only for the BSL phonological task. This task, we argue, placed greater demands on  
43 visuospatial processing than the other two tasks. In hearing signers, enhanced activation  
44 was absent in both left and right STC during all three tasks. Lateralisation analyses  
45 demonstrated that the effect of deafness was more task-dependent in the left than the right  
46 STC whereas it was more task-independent in the right than the left STC. These findings  
47 indicate how the absence of auditory input from birth leads to dissociable and altered  
48 functions of left and right STC in deaf participants.

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50

51

52 Significance Statement

53

54         Those born deaf can offer unique insights into neuroplasticity, in particular in  
55 regions of superior temporal cortex (STC) that primarily respond to auditory input in  
56 hearing people. Here we demonstrate that in those deaf from birth the left and the right  
57 STC have altered and dissociable functions. The right STC is activated regardless of  
58 demands on visual processing. In contrast, the left STC is sensitive to the demands of  
59 visuospatial processing. Furthermore, hearing signers, with the same sign language  
60 experience as the deaf participants, did not activate the STCs. Our data advance current  
61 understanding of neural plasticity by determining the differential effects that hearing status  
62 and task demands can have on left and right STC function.

63

64 Introduction

65 The brain is capable of considerable experience dependent plasticity. Unique insight  
66 into the extent of this plasticity in the human brain is provided by those born severely or  
67 profoundly deaf. A robust and replicated finding is that, when those born congenitally  
68 deaf are processing visual stimuli, they show enhanced activation, relative to hearing  
69 participants, in regions of the superior temporal cortex (STC), that respond to auditory  
70 input in hearing people. The aim of the current study was to investigate how auditory  
71 experience influences the function of the left and right STC.

72 Prior studies have shown stronger activation in the right STC in deaf than hearing  
73 participants in response to a wide range of non-verbal visual stimuli such as moving dot  
74 arrays (Finney et al., 2001; Fine et al., 2005; Vachon et al., 2013), arrows (Ding et al.,  
75 2015), flashes (Bola et al., 2017) and static and moving sinusoidal gratings (Shiell et al.,  
76 2014). In contrast, in left STC enhanced activation in deaf compared to hearing  
77 participants appears to be highly stimulus and task dependent. For example, it is observed  
78 in response to sign language stimuli during sign target detection (Capek et al., 2010;  
79 Cardin et al., 2013) and semantic anomaly detection even when sign language experience  
80 is matched across deaf and hearing groups (MacSweeney et al., 2002; MacSweeney et al.,  
81 2004). However, it has not been observed during spoken language tasks on written words  
82 (Waters et al., 2007; Emmorey et al., 2013), pictures (MacSweeney et al., 2008;  
83 MacSweeney et al., 2009) or speechreading (Capek et al., 2010 but see Capek et al., 2008)  
84 even though speechreading, like sign language, involves the perception of linguistically  
85 complex, moving visual stimuli.

86

87

88 Plausibly, the enhanced left STC activation in deaf participants in response to sign  
89 language could reflect the demands on visuospatial working memory that are made during  
90 sign language processing but not when performing speech-based tasks. In addition to the  
91 right STC activation, Ding et al. (2015) have also reported the contribution of the left STC  
92 to visuospatial working memory in deaf participants during a visuospatial working  
93 memory task for coloured arrows (i.e. non-verbal visual stimuli). Importantly this left STC  
94 activation was observed only during the maintenance and recognition phases of the task,  
95 not during the encoding phase when the visual stimulus was present (see MacSweeney  
96 and Cardin, 2015 for commentary). This account can explain why Bola et al. (2017) also  
97 reported increases in the left (and right) STC activation in deaf participants performing a  
98 visual rhythm working memory task involving sequences of flashes.

99 To dissociate sensory, visuospatial, semantic and phonological processing in left and  
100 right STC, we engaged deaf and hearing signers in three different tasks in response to  
101 pictures of two objects. Visual imagery and visuospatial working memory were engaged  
102 during a British Sign Language (BSL) phonological judgement task (MacSweeney et al.,  
103 2008). This task required participants to decide whether the BSL signs for the two objects  
104 depicted shared a BSL phonological parameter (handshape or location), which are used to  
105 describe the sublexical structure of signs (Stokoe, 1960; Brentari, 1998; Sandler, 2006).  
106 In addition, the same participants were engaged in semantic and perceptual tasks that  
107 placed minimal demands on visual imagery and visuospatial working memory while  
108 keeping the stimulus presentation constant.

109 To dissociate auditory experience from sign language experience, and to examine any  
110 possible interactions between hearing and sign language experience, we included two  
111 groups of deaf participants who were either early or late sign language learners and two



112 groups of hearing participants who were also either early or late sign language learners. In  
113 line with previous studies, we predicted greater activation in deaf than hearing participants  
114 in right STC, regardless of task. In contrast, in the left STC we expected task specific  
115 effects of deafness, with a stronger effect on the BSL phonological task than the semantic  
116 or visual tasks.

117

## 118 Materials and Methods

### 119 *Participants*

120 Sixty participants were scanned. All participants knew BSL. All had normal or  
121 corrected-to-normal vision and all gave informed, written consent to participate in the  
122 study, which was approved by the University College London Research Ethics  
123 Committee. One participant was excluded due to a data acquisition problem. A further 11  
124 participants were excluded because of excessive head motion in the scanner (i.e., > a  
125 voxel size = 3 mm in translation or the equivalent in rotation calculated with 65mm as the  
126 cortical distance (Wilke, 2014)). Thus, data from 48 participants were included in the  
127 analyses. All participants were right-handed (measured by the Edinburgh inventory;  
128 (Oldfield, 1971)) and without any known neurological abnormality.

129 Four participant groups were tested: [1] Deaf native signers who learnt BSL from  
130 birth (henceforth DE (deaf early); n=11 (male=4)); [2] deaf non-native signers who began  
131 to learn BSL aged 15 or older (henceforth DL (deaf late); n=12 (male=6)); [3] hearing  
132 native signers who learnt BSL from birth (henceforth HE (hearing early); n=13 (male=1));  
133 [4] hearing non-native signers who began to learn BSL aged 15 or older (henceforth HL  
134 (hearing late); n=12 (male=5)). The mean age of each of the groups was – DE: 35:03 years  
135 (range: 26:11 – 59:10 years); DL: 39:06 years (range: 29:01 – 55:05 years); HE: 36:01

136 years (range: 20:03 – 60:00 years); HL: 41:10 years (range: 25:10 – 56:02 years). There  
137 were no significant age differences between groups ( $F(3,44)=1.168, p=.333, \eta^2 = .074$ ).

138 To facilitate group matching, participants were tested on the BSL grammaticality  
139 judgement task (Cormier, et al., 2012), on performance IQ (PIQ; block design subtest of  
140 the WAIS-R), on reading attainment (Vernon-Warden, 1996) and on English vocabulary  
141 (shortened version of the Boston Naming Test; Kaplan and Goodglass, 1983). The BSL  
142 grammaticality judgement data were missing from two DE and one DL participants; the  
143 reading attainment data were missing from two HE and one DL participants; and the  
144 English vocabulary data were missing from one HL participant. There were no significant  
145 differences among the groups on the BSL grammaticality judgement task ( $F(3,41)=1.322,$   
146  $p=.280, \eta^2 = .088$ ), PIQ ( $F(3,44)=1.086, p=.365, \eta^2 = .069$ ) or English vocabulary  
147 ( $F(3,43)=1.363, p=.267, \eta^2 = .087$ ). However, there were group differences on reading  
148 attainment ( $F(3,41)=8.989, p<.001, \eta^2 = .397$ ) such that HL scored significantly better  
149 than HE ( $t(21)=3.433, p=.002, d=1.433$ ), DE ( $t(21)=4.610, p<.001, d=1.924$ ) and DL  
150 ( $t(21)=4.397, p<.001, d=1.835$ ). There were no significant differences in reading  
151 attainment between the HE, DE and DL groups.

152 All deaf participants reported being born severely or profoundly deaf. Past audiogram  
153 data was available for only half of the participants (DE – 5/11; DL 6/12). The mean  
154 hearing loss in the better ear for the DE participants was 91.2 dB; range: 81 - 105. The  
155 mean hearing loss in the DL group was 102.0 dB; range: 91 – 116. See Table 1 for a  
156 summary of participant characteristics. The use of hearing aids varied across deaf  
157 participants. The preferred language at the time of the experiment was BSL for all deaf  
158 participants except one. The details of hearing aid use in deaf participants, language  
159 experience when growing up and preferred language in adulthood are detailed in Table 2.

160

161 [Insert Table 1 about here]

162 [Insert Table 2 about here]

163

164 *Experimental design*

165 Two between-subject factors were included: hearing status (deaf vs. hearing) and age of  
166 sign language acquisition (age of acquisition: early vs. late). In addition, a within-subject  
167 factor, Task, was included with three levels (BSL phonological, semantic, visual  
168 judgement). This resulted in a balanced,  $2 \times 2 \times 3$  (hearing status  $\times$  age of acquisition  $\times$   
169 task) factorial design.

170

171

172 *Stimuli and task*

173

174 The stimuli consisted of 200 pictures which were recombined to form 300 different  
175 picture pairs. Three picture pair sets were established such that 100 pairs were used in  
176 each of the three tasks: phonological, semantic and visual judgement. Within each picture  
177 set, 50 pairs were established to form ‘yes’ trials and 50 to form ‘no’ trials. Overall this  
178 design ensured that the same pictures were used across all three tasks. All 200 pictures  
179 were used in the phonological and semantic tasks, whereas only 150 of the pictures were  
180 used in the visual task due to the nature of the ‘same picture?’ task (see below).

181 Of the 200 pictures, 194 were black and white line drawings depicting high-  
182 familiarity nouns, of which all but one (‘dream’) was concrete. The remaining six pictures  
183 were coloured squares representing colour names. Half of the pictures were from the

184 Snodgrass and Vanderwart (1980) normed picture set. The other half was sourced from a  
185 range of picture-naming projects and were selected or adapted to match the visual  
186 characteristics of the Snodgrass and Vanderwart set.

187

188 Phonological judgement task - 25 picture pairs were established in which the BSL label  
189 for the picture overlapped in handshape and 25 which overlapped in hand location. These  
190 are two of the phonological parameters of signed languages (Sandler and Lillo-Martin,  
191 2006). A further 50 picture pairs were established as ‘no’ trials’ in which the BSL labels  
192 did not overlap in any phonological parameter and the items were not semantically related.

193 Semantic judgment task - The 200 picture stimuli were recombined to form 50 category-  
194 related pairs (e.g., ‘pear—banana’, ‘drum—guitar’, ‘sun—moon’) and 50 unrelated pairs.  
195 These stimuli were piloted with 15 hearing native speakers of English. Only pairs in  
196 which 12 or more of the pilot participants reported a category relationship were used as  
197 ‘yes’ stimuli in the fMRI study. Similarly, ‘no’ trials were only used if a minimum of 14  
198 of the 15 pilot participants agreed that the pictures were unrelated.

199 Visual task - In the visual matching (‘same?’) condition, 50 of the 200 pictures appeared  
200 in 50 same-picture pairs (e.g., ‘sun—sun’) and 100 appeared in 50 different picture pairs  
201 (e.g., sun – pear). Examples of the stimuli are shown in Figure 1.

202

203

204 [Insert Figure 1 about here]

205

206

207           Due to lexical variation in BSL (Schembri et al., 2010), it was important to show  
208 participants all experimental pictures before the fMRI experiment to ensure that they used  
209 the desired BSL label, to facilitate the BSL phonological task. For each participant, there  
210 were only a few pictures where it was necessary to ask participants to base their decisions  
211 on signs that, although part of the BSL lexicon, were not the signs they usually used for  
212 the item.

213

#### 214           *Procedure*

215 Participants performed three judgement tasks: BSL phonological, semantic and visual. In  
216 the BSL phonological task, participants were required to press a button when the BSL  
217 labels for the two pictures shared a sign phonological parameter. In separate blocks  
218 participants were required to detect shared handshape or shared location. In the current  
219 study, data are combined to form the ‘BSL phonological judgement’ condition. The data  
220 contrasting handshape and location decisions will be reported separately. In the semantic  
221 task, participants were required to press a button when the picture pairs came from the  
222 same category (e.g., elephant/ donkey). In the visual task participants judged whether the  
223 pictures presented were the same or different.

224

225 For all participants, the right index finger was used to respond to ‘yes’ trials. ‘No’ trials  
226 did not require a response. Half the trials in each condition were ‘yes’ trials and half were  
227 ‘no’ trials. Participants practiced the tasks, on stimuli not presented in the scanner,  
228 immediately prior to the fMRI experiment.

229

230 Each participant completed four fMRI runs (7 mins each). Each run consisted of  
231 15 x 21-sec blocks of which five were BSL phonological decision blocks, five were  
232 semantic decision blocks and five were visual matching blocks. The order of presentation  
233 of conditions was pseudorandomised across runs. Each block began with a 1-sec printed  
234 English task prompt (either ‘handshape?’ or ‘location?’ for the BSL phonological  
235 decision, ‘related?’ for the semantic decision, or ‘same?’ for the visual decision). This was  
236 followed by five picture-pair presentations, each with a 3.5-sec exposure duration and an  
237 inter-stimulus interval of 500 msec. Task blocks were separated by baseline blocks of  
238 crosshair fixation:  $13 \times 6$  sec blocks; and two longer 13.5-sec fixation blocks positioned in  
239 the middle and towards the end of the run. Stimuli were projected onto a screen  
240 positioned at the top of the scanner bore. Participants viewed the stimuli via a mirror  
241 placed on the MRI head coil.

242

#### 243 *MRI acquisition*

244 Anatomical and functional images were acquired from all participants using a  
245 Siemens 1.5-T Sonata scanner. Anatomical T1-weighted images were acquired using a 3-  
246 D MDEFT (modified driven equilibrium Fourier transform) sequence. One hundred and  
247 seventy-six sagittal partitions with an image matrix of  $256 \times 224$  and a final resolution of  
248 one mm<sup>3</sup> were acquired (repetition time (TR): 12.24 msec; echo time (TE): 3.5 msec;  
249 inversion time (TI): 530 msec). Structural scans indicated that our participants were free  
250 from gross neurological abnormalities.

251 Functional T2\*-weighted echo-planar images with BOLD contrast comprised 38  
252 axial slices of 2 mm thickness (1 mm gap), with  $3 \times 3$  mm in-plane resolution. One  
253 hundred and thirty-four volumes were acquired per run (repetition time (TR): 3.42 sec;

254 echo time (TE): 50 msec; flip angle = 90°). TR and stimulus onset asynchrony were  
255 mismatched, allowing for distributed sampling of slice acquisition across the experiment  
256 (Veltman et al., 2002), which obviates the need for explicit “jittering”. To avoid Nyquist  
257 ghost artifacts, a generalized (trajectory-based) reconstruction algorithm was used for data  
258 processing. After reconstruction, the first six volumes of each session were discarded to  
259 ensure tissue steady-state magnetization.

260

### 261 *Statistical Analysis*

262 Behavioral data were analysed in a  $2 \times 2 \times 3$  ANOVA with hearing status (deaf,  
263 hearing), the age of BSL acquisition (early, late) as between-subject factors and task (BSL  
264 phonological, semantic, visual) as a within-subject factor. The  $d'$  scores, accuracy and  
265 reaction times (RTs) were the dependent measures. Where Mauchly's test indicated  
266 significant non-sphericity in the data, a Greenhouse–Geisser correction was applied. When  
267 there was a main effect of task or interaction effects with task, planned comparisons were  
268 carried out using paired t-tests to evaluate differences between: i) the BSL phonological  
269 and the semantic tasks; ii) the semantic and the visual tasks and iii) the BSL phonological  
270 and the visual tasks. For the calculation of the  $d'$  scores, corrections of  $\pm 0.01$  were made  
271 since some subjects had the hit rate of 1 and/or the false alarm rate of 0. RTs were  
272 measured for go trials only and were recorded from the onset of the stimulus. Anticipatory  
273 responses ( $< 200$ ms) were trimmed ( $N = 9$ ; 0.05% of all the trials across participants).

274

275 The imaging data were processed using SPM12 (Wellcome Trust Centre for  
276 Neuroimaging, London UK; <http://www.fil.ion.ucl.ac.uk/spm/>). All functional volumes  
277 were spatially realigned and unwarped in order to adjust for minor distortions in the B0

278 field due to head movement (Andersson et al., 2001). All functional images were  
279 normalized to the Montreal Neurological Institute (MNI) space (maintaining the original  
280  $3 \times 3 \times 3$  mm resolution). Functional images were then smoothed using an isotropic 6 mm  
281 full-width half-maximum (FWHM) Gaussian kernel.

282 First-level fixed-effects analyses were based on a least squares regression analysis  
283 using the general linear model in each voxel across the whole brain. Low-frequency noise  
284 and signal drift were removed from the time series in each voxel with high-pass filtering  
285 (1/ 128 Hz cutoff). Residual temporal autocorrelations were approximated by an AR(1)  
286 model and removed. At the first level, the onsets of stimuli (3.5 secs) were modelled as  
287 epoch-related responses (for the exact duration of the stimuli) and convolved with a  
288 canonical haemodynamic response function. Correct trials for each of the three conditions  
289 over four sessions and the errors were modelled separately. Button press manual responses  
290 were modelled as event-related responses and convolved with a canonical haemodynamic  
291 response function. Fixation was not modelled and served as an implicit baseline. The  
292 contrasts of interest were each experimental condition (BSL phonological, semantic, and  
293 visual) relative to fixation, averaged over sessions.

294 At the second-level, a random-effects analysis included the contrast images for the  
295 three task conditions relative to fixation (within-subject) for each of the four (2x2) groups  
296 (between-subject), resulting in  $2 \times 2 \times 3$  ANOVA with hearing status (deaf, hearing), the  
297 age of BSL acquisition (early, late) as between-subject factors and task (BSL  
298 phonological, semantic, visual) as a within-subject factor with a correction for non-  
299 sphericity. The RTs, which may have contributed to the task effects, were not included in  
300 the imaging analyses since we were interested in the task difference.



301 We identified the effects in the left STC and the right STC separately. We first  
302 identified the effects of task modulation. Given the step-wise increase on the linguistic  
303 task demands, we specifically looked for the BSL phonological task > the semantic task;  
304 and the semantic task > the visual task. We then established whether deaf signers  
305 activated more than the hearing signers across tasks (i.e. the effect of deafness). Finally,  
306 we identified whether the effect of deafness was dependent on task and on age of BSL  
307 acquisition. We report activation as significant at voxel-level inference of  $p < .05$ , family  
308 wise error corrected for multiple comparisons at the whole brain level ( $Z > 4.76$ ). For  
309 effects within the left or right STC, we also report activation at an uncorrected level of  
310  $p < .001$  since we had a priori hypotheses regarding the function of these regions.

311 Lateralisation was assessed using the bootstrapping procedure implemented within  
312 the LI toolbox (Wilke and Schmithorst, 2006; Wilke and Lidzba, 2007) in SPM. This is a  
313 robust tool that deals with the threshold dependency of assessing laterality from  
314 neuroimaging data (Bradshaw et al., 2017). We assessed lateralisation for a main effect of  
315 group and interactions of group and tasks. The contrasts used were: 1) deaf > hearing; 2)  
316 deaf > hearing by phonological task > semantic task and 3) deaf > hearing by  
317 phonological task > visual task. Ten thousand lateralisation indices (LIs) were calculated  
318 from one hundred bootstrapped resamples of voxel values in each hemisphere, at multiple  
319 thresholds. Since this analysis is based on a bootstrapping procedure, it does not require a  
320 fixed threshold or correction for multiple comparisons. Resulting LIs were plotted and the  
321 weighted mean, which gives greater weighting to higher thresholds, was calculated. A  
322 built-in temporal mask, which covers the entire temporal cortices, was selected as an  
323 inclusive mask. No exclusion mask was used. Analyses were conducted without clustering  
324 or variance weighting. Weighted laterality values  $\geq +0.2$  (left) or  $\leq -0.2$  (right) indicate

325 significant lateralisation (Wilke et al., 2006; Wilke and Schmithorst, 2006; Lebel and  
326 Beaulieu, 2009; Lidzba et al., 2011; Badcock et al., 2012; Nagel et al., 2013; Pahs et al.,  
327 2013; Gelinas et al., 2014; Norrelgen et al., 2015; Evans et al., 2016). We also report the  
328 trimmed mean, which is calculated from the central 50% of all the LIs, for completeness.

329

330

331 *Results*

332 *Behavioural data*

333 The  $d'$  scores showed that there was a significant difference in response sensitivity  
334 as a function of tasks ( $F(2,88)=397.189, p<.001, \eta^2 = .900$ ). Planned t-tests confirmed that  
335  $d'$  for the BSL phonological task was significantly lower than the semantic task  
336 ( $t(47)=20.386, p<.001, d=2.943$ ) and the visual task ( $t(47)=26.924, p<.001, d=3.885$ ). In  
337 addition,  $d'$  for the semantic task was significantly lower than the visual task ( $t(47)=7.334,$   
338  $p<.001, d=1.059$ ). However, response sensitivity did not differ across hearing status  
339 ( $F(1,44)=.665, p=.419, \eta^2=.015$ ) or age of acquisition ( $F(1,44)=.137, p=.713, \eta^2=.003$ )  
340 and the interaction of these two factors was not significant ( $F(1,44)=3.243, p=.079, \eta^2$   
341  $=.069$ ). Other interactions were also nonsignificant (all  $p>.267$ ).

342 A main effect of task was also significant for reaction times (RTs) ( $F(1.559,$   
343  $68.601)=1530.809, p<.001, \eta^2=.972$ ). The RTs were longer for the BSL phonological  
344 task than the semantic task ( $t(47)=34.920, p<.001, d=5.042$ ) and the visual task  
345 ( $t(47)=42.766, p<.001, d=6.174$ ) and for the semantic task than the visual task  
346 ( $t(47)=24.457, p<.001, d=3.532$ ). There were no main effects of hearing status ( $F(1,$   
347  $44)=1.362, p=.249, \eta^2=.030$ ) or age of acquisition ( $F(1, 44)=3.205, p=.080, \eta^2=.068$ ).  
348 In the RT data however, there was a significant task x age of acquisition interaction

349 ( $F(1.559,68.601)=3.828$ ,  $p=.036$ ,  $\eta^2=.080$ ). Post-hoc t-tests confirmed that the  
350 participants who learnt BSL late (HL & DL) were significantly slower than those who  
351 learnt BSL early (HE & DE) on the BSL phonological task (2129.92 vs. 1979.25,  
352  $t(46)=2.136$ ,  $p=.038$ ,  $d=.617$ ) but not on the semantic (1201.17 vs. 1127.75,  $t(46)=1.227$ ,  
353  $p=.226$ ,  $d=.354$ ) or the visual tasks (744.38 vs. 720.33,  $t(46)=.637$ ,  $p=.527$ ,  $d=.184$ ). The  
354 behavioural data are illustrated in Figure 2. Although Figure 2 suggests that this  
355 interaction might be driven by the deaf participants, there was no significant three-way  
356 interaction ( $F(1.559,68.601)=2.343$ ,  $p=.116$ ,  $\eta^2=.051$ ). The interaction of hearing status  
357 and age of acquisition was also not significant ( $F(1,44)=2.381$ ,  $p=.130$ ,  $\eta^2=.051$ ).

358 In summary, the behavioural data suggest that the BSL phonological task was  
359 more demanding than the semantic task, which in turn was more demanding than the  
360 visual task. Moreover, the effect of learning BSL late was evident in reaction times during  
361 the BSL phonological task only. There was no effect of hearing status on behavioural  
362 performance on the tasks or interaction between hearing status and any other factors.

363

364 [Insert Figure 2 about here]

365

366

367 *fMRI data*

368 Left STC

369 There were group by task interactions in the left STC, significant at  $p<.05$  FWE  
370 corrected (see Table 3 for details). These indicated enhanced activation in deaf relative to  
371 hearing signers only for the BSL phonological task (Figure 3). The location of the  
372 enhanced left STC activation was in the posterior superior temporal gyrus and sulcus and

373 did not include Heschl's gyrus. Rather, activation was within the higher-order auditory  
374 cortex Te 3, defined by the SPM Anatomy Toolbox Version 2.2b (Eickhoff et al., 2005;  
375 Eickhoff et al., 2006; Eickhoff et al., 2007). Within the deaf participants, left STC  
376 activation was significantly greater for the BSL phonological task than the semantic task  
377 or the visual task. The difference in activation during the semantic and visual tasks was  
378 also significant (see Table 3 for details). The main effect of deafness, across the three  
379 tasks, was only significant in the left STC at the  $p < .001$  uncorrected level [ $x = -66$ ,  $y = -$   
380  $34$ ,  $z = +5$ ;  $Z = 3.55$ ,  $k = 5$ ].

381 A very different response pattern was observed in the left STC in hearing signers.  
382 During the BSL phonological task, hearing signers showed deactivation, although this was  
383 only significant at the  $p < .001$  uncorrected level [ $x = -66$ ,  $y = -31$ ,  $z = +5$ ;  $Z = -3.47$ ,  
384  $k = 1104$ ]. Although deactivation for the BSL phonological task was numerically greater  
385 than the semantic task, which in turn was numerically greater than the visual task, there  
386 was no significant difference across tasks (see Table 3 for details).

387 There was no main effect of age of acquisition in left STC ( $p > .001$  uncorrected).  
388 There were no significant age of acquisition by task interactions and no three way  
389 interactions between age of acquisition, group and task.

390

391 [Insert Table 2 about here]

392

393

394 Right STC

395 Across tasks, the right STC showed significantly greater activation in the deaf than  
396 hearing signers, [ $x = +66$ ,  $y = -34$ ,  $z = +8$ ;  $Z = 5.35$ ,  $p = .002$ ,  $k = 14$  FWE corrected]. This task

397 independent effect of deafness in the right STC was observed in the homologue to the  
398 region showing a task-*dependent* effect of deafness in the left STC (see Figure 3).

399         There were no significant group by task interactions at  $p<.05$  FWE corrected.  
400         However, these interactions were present at a lower threshold of  $p<.001$  uncorrected, (see  
401         Table 4). The effect of age of acquisition (late > early) in the right STC, was significant  
402         only at  $p<.001$  uncorrected [ $x=+57$ ,  $y=-34$ ,  $z=+11$ ;  $Z=3.19$ ,  $k=3$ ]. Late learners showed  
403         greater activation (deaf) or reduced deactivation (hearing) than early learners. None of the  
404         interactions between age of acquisition and task, age of acquisition and group or age of  
405         acquisition, group and task reached significance ( $p>.001$  uncorrected).

406

407   [Insert Table 4 about here]

408

409

410   [Insert Figure 3 about here]

411

412

413         Hemispheric differences

414         At the corrected level ( $p<.05$  FWE), the data demonstrated significant group by  
415         task interactions in the left STC (deaf > hearing in the phonological task only) and a  
416         significant group effect in the right (deaf > hearing in all three tasks). However, assessing  
417         laterality effects is, amongst other things, dependent on the statistical threshold used.  
418         Indeed, at the lower threshold of  $p<.001$  uncorrected, we found group by task interactions  
419         in the right STC and a main effect of group in the left STC. In order to determine whether  
420         auditory experience differentially influences the function of left and right STC irrespective

421 of statistical thresholds, we performed additional analyses to directly test for the  
422 hemispheric differences in STC. Boot strapped laterality analyses (Wilke and Schmithorst,  
423 2006; Wilke and Lidzba, 2007) confirmed that the main effect of group was right  
424 lateralised (weighted mean =  $-0.53$ ; trimmed mean =  $-0.35$ ) while both interaction effects  
425 involving group and task were left lateralised (phon > sem: weighted mean =  $0.49$ ,  
426 trimmed mean =  $0.27$ ; phon > vis: weighted mean =  $0.53$ , trimmed mean =  $0.32$ ).  
427 Lateralisation index values are plotted in Figure 4.

428

429

430

431 [Insert Figure 4 about here]

432

433

434

435 Other regions

436 Deaf signers also showed greater activation than hearing signers, across all tasks,  
437 in visual processing regions (see Table 5 & Figure 3) even though the stimuli, accuracy  
438 and response times did not differ for deaf and hearing participants. No regions were  
439 activated significantly more in hearing than deaf participants.

440

441 [Insert Table 5 about here]

442

443

444

445 Summary

446 Deaf participants showed increased activation relative to hearing participants in both left  
447 and right STC. This effect was greatest during the BSL phonological task in left STC. In  
448 contrast, enhanced activation in the deaf group was not task dependent in the right STC.  
449 Analyses directly testing the hemispheric differences confirmed that the interaction of  
450 deafness and task was more left lateralised, whereas the main effect of deafness was more  
451 right lateralised.

452

453

454 Discussion

455       Understanding how biological and environmental constraints influence neural  
456 plasticity is fundamental to a complete understanding of the brain. Unique insights into  
457 these questions can be gained from working with those who are born profoundly deaf.  
458 Unlike research with deaf animal models (e.g., Lomber et al., 2010; Kral et al., 2016),  
459 research with deaf humans must take into account the influence of accessing language  
460 primarily through the visual modality and the age of acquisition of that visuospatial  
461 language in order to fully understand experience dependent neural plasticity (see  
462 Campbell et al., 2014). Prior studies have shown that activation in the superior temporal  
463 cortices (STC) in response to sign language stimuli is significantly greater in deaf native  
464 signers than hearing native signers (e.g., MacSweeney et al., 2002; MacSweeney et al.,  
465 2004). Here we investigated the functional role of the left and right STC in deaf signers by  
466 manipulating task demands and the age at which sign language was acquired.

467       Our results reveal that deaf and hearing signers show contrasting effects in the  
468 STC during BSL phonological decisions on pictures of objects. The region showing

469 differential effects included the posterior superior temporal gyrus and sulcus but excluded  
470 Heschl's gyrus. Deaf signers showed STC activation, which was absent in hearing signers.  
471 These contrasting effects were observed even though the stimuli and task instructions  
472 were identical for all participants, and even though there was no significant difference in  
473 response times for the deaf and hearing participants, all of whom had similar sign  
474 language experience.

475

476 Our results also differentiate responses in the left and right STC. Specifically, left  
477 STC was more sensitive to task than deafness while right STC was more sensitive to  
478 deafness regardless of task. We consider whether and how the left and right STC  
479 contribute to visual cognition, in those born deaf and in those born hearing.

480

481

482 *Left STC function in those born deaf*

483 The task dependent effects in left STC provide clues to its computational function.  
484 Activation increases were strongest when the demands on visual imagery and visuospatial  
485 working memory were highest. This observation [at  $x=-66$ ,  $y=-31$ ,  $z=+5$  in MNI space]  
486 is consistent with prior evidence that deaf participants show increased activation in the  
487 similar part of STC [ $x=-51$ ,  $y=-33$ ,  $z=+6$  in MNI space] during the maintenance and  
488 recognition phases of a visuospatial working memory task with nonverbal stimuli (Ding et  
489 al., 2015). It also falls within the cytoarchitectonic region (Te 3) where Bola et al. (2017)  
490 found enhanced STC activation in deaf participants during a visual rhythm working  
491 memory task involving sequences of flashes. The contribution of left STC to visuospatial  
492 processing in deaf participants might therefore explain responses observed in response to



493 both verbal and nonverbal stimuli. In hearing people, in addition to speech recognition  
494 and phonological processing (Hickok, 2009; Okada et al., 2010; Evans et al., 2014), this  
495 part of the left STC has been implicated in auditory working memory (Leff et al., 2009)  
496 and auditory imagery (McNorgan, 2012). Demonstrating the involvement of the left STC  
497 in visuospatial processing in those born deaf complements what has been observed in  
498 congenitally deaf cats. For example, Lomber et al. (2010) has shown that parts of auditory  
499 cortex that are usually involved in identifying auditory location in hearing cats are  
500 recruited to identify visual location in deaf cats; while regions involved in identifying  
501 auditory movement in hearing cats are recruited to process visual motion in deaf cats.

502         We found no evidence for the influence of age of acquisition in the left STC  
503 activation. At first glance, this may appear to be inconsistent with prior studies showing  
504 early sign language acquisition can improve nonverbal working memory (Marshall et al.,  
505 2015) and sign language processing - particularly grammaticality judgements (Mayberry  
506 et al., 2011; Cormier et al., 2012; Henner et al., 2016). Earlier sign language acquisition  
507 has also been reported to be related to *increased* left STC activation (Mayberry et al.,  
508 2011). However, the effect of age of acquisition on both behaviour and brain activation is  
509 highly task dependent. For example, Mayberry et al. (2011) did not see an advantage of  
510 early sign language acquisition in behavioural performance when their participants were  
511 engaged in a phonemic-hand judgment task, nor an effect on brain activation during  
512 passive viewing of a still image of the signer. In addition, age of acquisition is often  
513 correlated with proficiency. In our study, we matched the sign language proficiency across  
514 those who learnt sign language early versus late, and this might explain why left STC  
515 activation was not influenced by age of acquisition in our participants. Future studies will

516 need to dissociate effects that are related to age of sign language exposure and, separately,  
517 to sign language proficiency.

518

519

520 *Left STC function in those born hearing*

521 While deaf signers showed enhanced left STC activation during the BSL  
522 phonological task relative to other tasks, hearing signers did not activate this region. This  
523 contrasting pattern was observed even though they had the same sign language experience  
524 and performance.

525 We propose that our hearing participants may have been suppressing distracting  
526 auditory information from the environment. Indeed, deactivation in sensory cortices when  
527 attending to another sensory input is a well-documented phenomena (e.g., Laurienti et al.,  
528 2002 but see Ding et al., 2015). For example, hearing non-signers have been shown to  
529 deactivate STC when performing a *visual* rhythm task (Bola et al., 2017) and also a visual  
530 imagery task (Zvyagintsev et al., 2013). Participants have also been shown to deactivate  
531 *visual* cortex while performing *auditory* spatial and pitch judgement tasks (Collignon et  
532 al., 2011). This modality specific deactivation allows the down regulation of potentially  
533 distracting sensory activity in other modalities, for example, scanner noise in hearing  
534 participants doing a visually demanding task. Although deactivation in hearing signers in  
535 the current study did not reach the threshold for statistical significance a similar  
536 explanation may explain the pattern observed in this group.

537 It is interesting that while hearing signers in the current study and hearing non-  
538 signers in Bola et al. (2017) did not activate the STC, hearing non-signers tested by Ding  
539 et al. (2015) showed positive activation. The potential cause of the discrepancy in STC  
540 deactivation in hearing participants between studies is unclear and requires investigation.

541

542 *Right STC function in those born deaf and those born hearing*

543 Unlike the left STC, deaf participants activated right STC irrespective of the task  
544 demands. Activation is therefore more likely to reflect bottom up, perceptual processing of  
545 visual stimuli than linguistic processing or visuospatial imagery or working memory  
546 demands. This is consistent with prior literature showing deafness related increases in  
547 right STC activation to a range of non-verbal visual stimuli such as moving dot arrays  
548 (Finney et al., 2001; Fine et al., 2005; Vachon et al., 2013) and static and moving  
549 sinusoidal gratings (Shiell et al., 2014). In contrast, hearing participants did not activate  
550 STC in response to any of the tasks.

551 There was also a main effect of age of sign language acquisition in the right STC  
552 (late > early). However, this had not been predicted and was significant only at an  
553 uncorrected level. Further studies are necessary to examine this potential effect.

554

555

556 *Hemispheric differences in STC in deaf signers*

557 Finally, we found that the main effect of group was right lateralised, with deaf  
558 signers demonstrating significantly greater activation than hearing signers. In contrast,  
559 interactions of group and task (deaf > hearing by BSL phonological task > semantic task;  
560 deaf > hearing by BSL phonological task > visual task) were left lateralised. These  
561 hemispheric differences were not reported in the Bola et al. (2017) study and only reported  
562 during the encoding phase of a visual memory task in the Ding et al. (2015) study. Since  
563 neither study used linguistic stimuli, it is likely that the hemispheric differences identified

564 in the current study reflect the additional contribution of the left STC to the increased  
565 visuospatial processing demands of the BSL phonological task.

566

567

568 *Conclusions*

569       Together our results from deaf and hearing signers suggest that the function of  
570 posterior STC, which includes the posterior superior temporal gyrus and sulcus but  
571 excludes Heschl's gyrus, changes with auditory experience. In those born hearing, left and  
572 right STC primarily responds to auditory stimuli and is suppressed, to some extent, during  
573 visual tasks. In contrast, when the STCs do not receive auditory input, left STC  
574 participates in tasks that require visuospatial processing and right STC participates in low-  
575 level visual processing, irrespective of visuospatial demands. As all our participants were  
576 proficient signers. Future studies are now required to determine how sign language  
577 knowledge and importantly, sign language proficiency, influence the strong effect of  
578 deafness on visuospatial processing in STCs that we have described here.

579

580

581

582 Figure legends

583

584 Figure 1: Stimulus examples. Top: BSL phonological task ‘Same handshape?’; Middle:  
585 Semantic task ‘Same category?’ Bottom: Visual task ‘Same picture?’

586

587 Figure 2: Behavioural results. Left panel = response sensitivity ( $d'$ ). Right panel = reaction  
588 times (msec). Both show a main effect of task; and a significant task by age of acquisition  
589 interaction on the reaction times only. Abbreviations: HE= hearing early; HL=hearing  
590 late; DE=deaf early; DL= deaf late; PHON= BSL phonological task; SEM= semantic task;  
591 VIS= visual task.

592

593 Figure 3: The main effect of deafness and the interaction of deafness and task at  $p < .05$   
594 FWE corrected (in red to yellow). At the FWE corrected level, these effects in STC were  
595 task-independent on the right (top panel) and task-dependent on the left (bottom panel).  
596 The bar plots of parameter estimates at these peaks are also shown. The error bars indicate  
597 the standard error. Abbreviations: PHON=phonological task; SEM=semantic task;  
598 VIS=visual task; HE=hearing early; HL=hearing late; DE=deaf early; DL=deaf late.

599

600 Figure 4: Lateralisation Index values for top: [deaf > hearing]; middle: [deaf > hearing by  
601 the BSL phonological task > the semantic task]; and bottom: [deaf > hearing by the BSL  
602 phonological task > the visual task] within temporal cortices.

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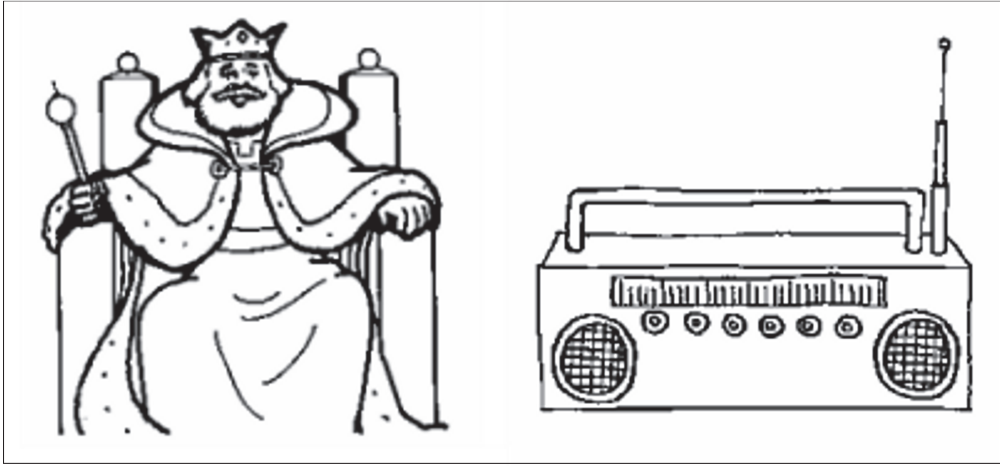
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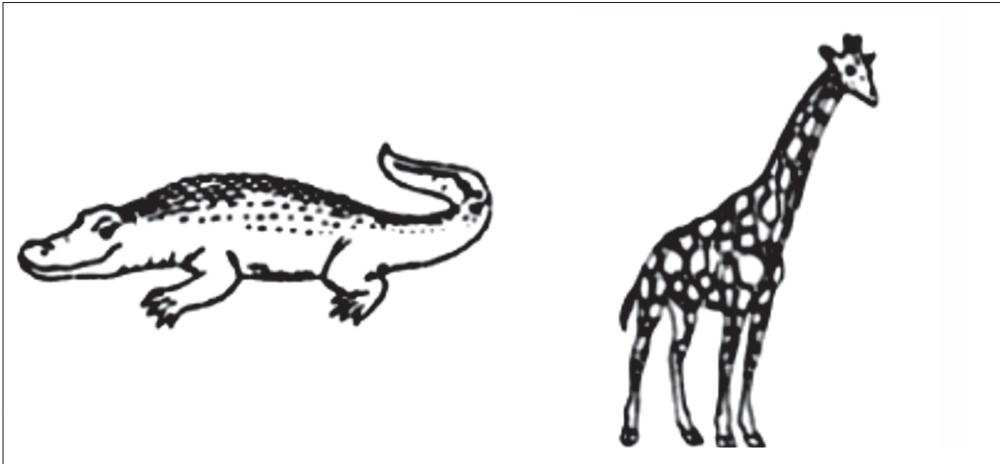
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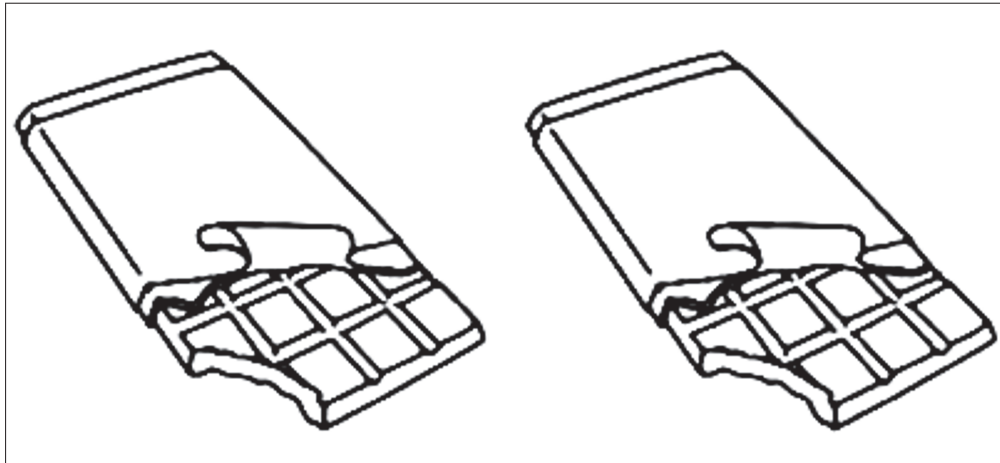
### BSL phonological task

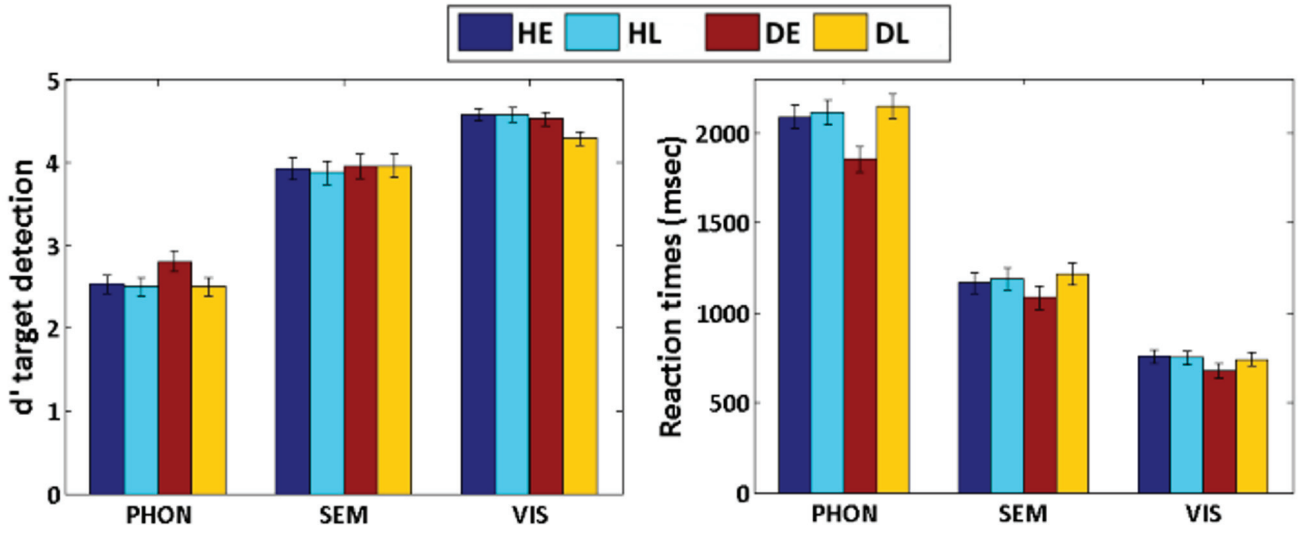


### Semantic task

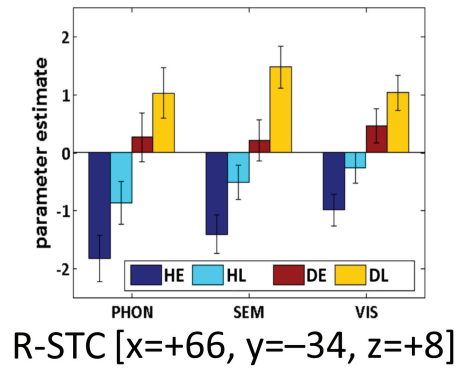
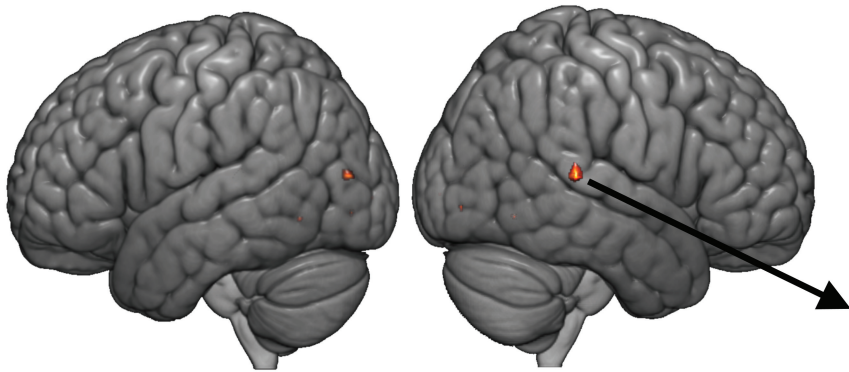


### Visual task

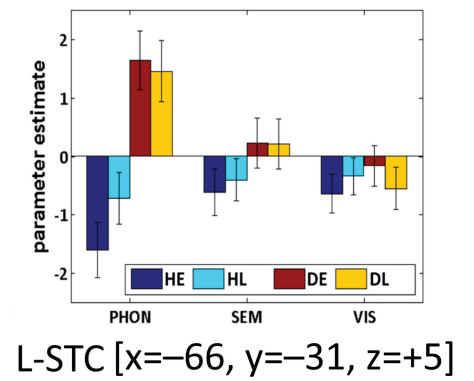
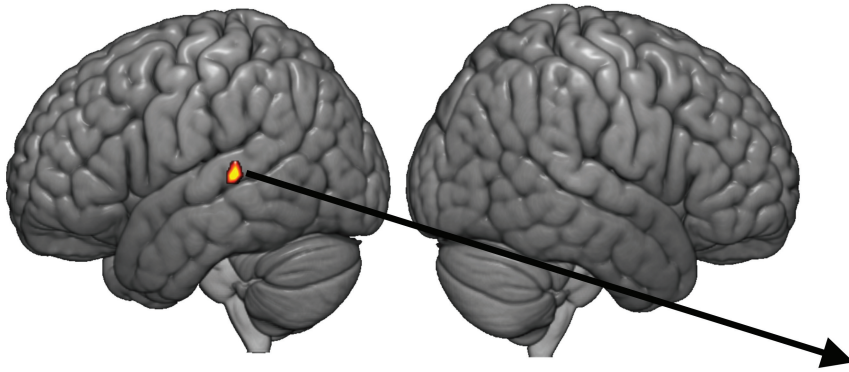




Group (Deaf > Hearing)



Group (Deaf > Hearing) x Task (Phon > Vis)





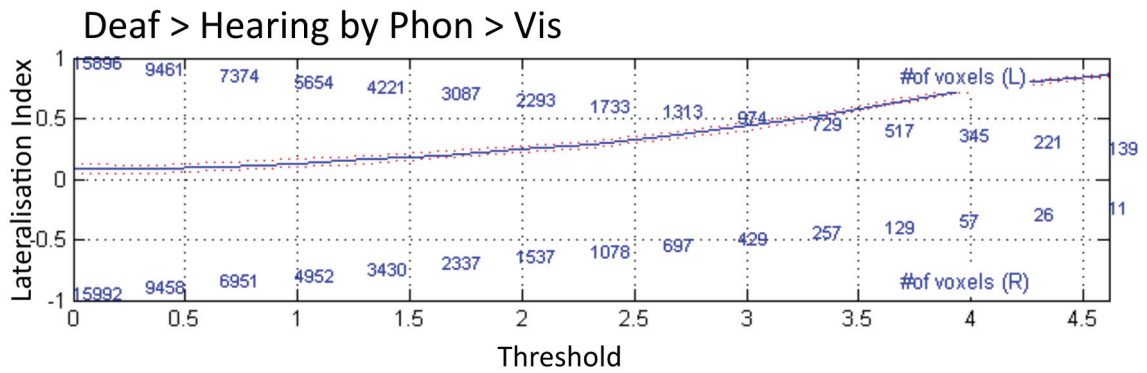
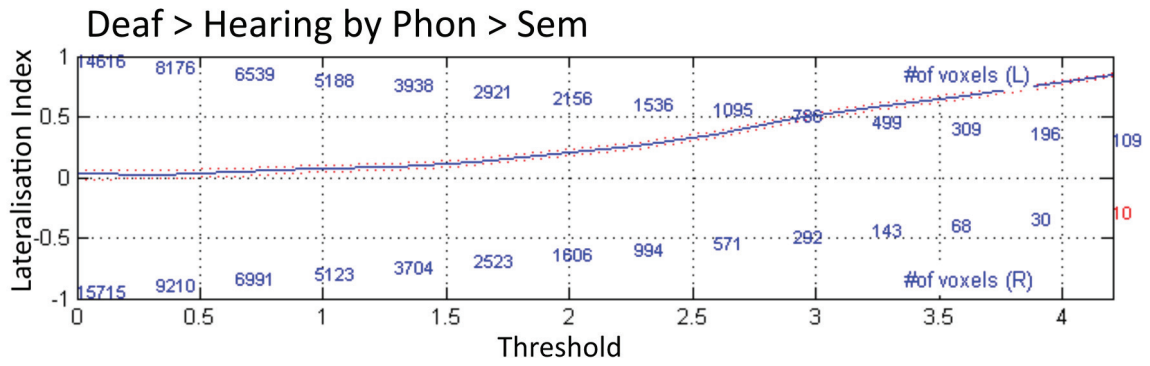
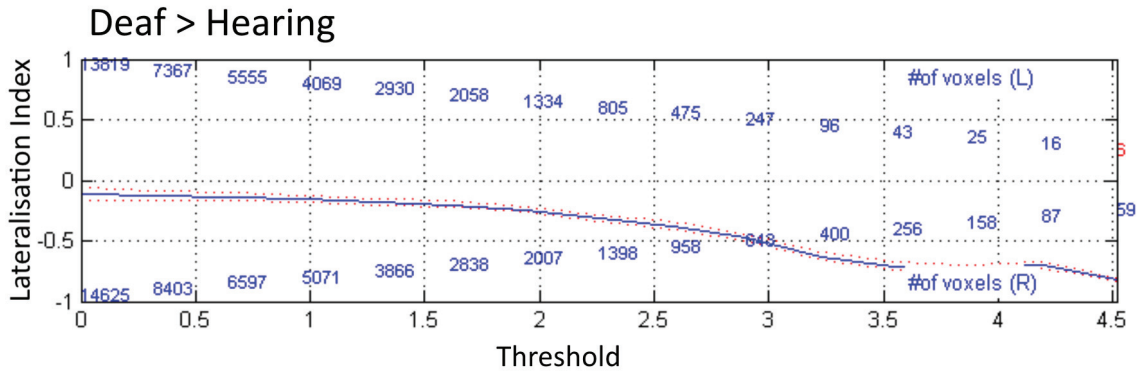


Table 1: Participant characteristics.

	Age (year:month)	Reading attainment (year:month)	Performance IQ (centile)	English vocabulary (Max = 30)	BSL grammaticality judgement (%)	Hearing level in the better ear (dB)
Hearing Early (N=13)	36:01 [10:10]	17:06 [1:11]	84.4 [8.1]	28.2 [1.6]	79.9 [8.5]	N/A
	20:03 – 60:00	14:08 – 21:00	61.0 – 91.0	24.0 – 30.0	66.7 – 95.0	
Hearing Late (N=12)	41:10 [8.08]	20:02 [1:10]	89.8 [9.6]	28.4 [1.6]	82.2 [6.3]	N/A
	25:10 – 56:02	15:08 – 22:00	63.0 – 98.0	26.0 – 30.0	73.3 – 90.0	
Deaf Early (N=11)	35:03 [11:03]	16:07 [1:11]	89.6 [11.3]	27.5 [1.2]	85.3 [8.5]	91.2 [10.7]
	26:11 – 59:10	13:06 – 18:06	66.0 – 99.0	25.0 – 29.0	66.7 – 91.7	81.0 -105.0
Deaf Late (N=12)	39:06 [7:09]	16:06 [2:02]	90.9 [10.7]	27.1 [2.3]	84.8 [5.4]	102 [11.5]
	29:01 – 55:05	13:0 – 19:06	66.0 – 99.0	22.0 – 30.0	76.7 – 96.7	91.0 – 116

**Table 2: The use of hearing aids and the experience of language use in deaf participants**

Participants	Use of hearing aids	Language	
		Used when growing up	Preferred
DE1	Data missing	Data missing	Data missing
DE2	Rarely	BSL/SSE	BSL
DE3	Every/all day	BSL/SSE/SpE	BSL
DE4	Data missing	Data missing	Data missing
DE5	In the past	BSL/SSE/SpE	BSL
DE6	Rarely	BSL	BSL
DE7	Never	BSL	BSL
DE8	Every/all day	BSL	BSL
DE9	Never	BSL	BSL
DE10	Data missing	Data missing	Data missing
DE11	Every/all day	BSL/SpE	BSL
DL1	In the past	SpE	BSL
DL2	Rarely	SpE	BSL
DL3	Never	SpE	BSL
DL4	In the past	SpE	BSL
DL5	Every/all day	SpE	BSL
DL6	Rarely	SpE	BSL
DL7	Sometimes	SpE	BSL
DL8	Never	SpE	BSL
DL9	Data missing	Data missing	Data missing
DL10	Every/all day	SSE/SpE	BSL
DL11	Every/all day	SpE	SpE
DL12	Every/all day	SpE	BSL

Table 3: Statistical details for hearing status and task interactions in left STC

	Deaf > Hearing					k		Deaf	Hearing
	x	y	z	Z-score	p-value			Z-sc. relative to baseline	
						FWE	p<.001		
						corrected	uncorrected	d	
BSL Phonological task	-66	-31	+5	5.26	<b>0.004 FWE</b>	<b>7</b>	<b>104</b>	4.14*	-3.47*
Semantic task	-63	-34	+5	2.70	n.s.	N/A	N/A	1.79	-.90
Visual task	-66	-28	+2	.71	n.s.	N/A	N/A	-0.27	-2.49
BSL Phonological > Semantic	-66	-31	+5	5.80	<0.001 FWE	<b>7</b>	<b>173</b>	5.20**	-3.08
BSL Phonological > Visual	-66	-31	+5	5.93	<0.001 FWE	<b>26</b>	<b>259</b>	5.77**	-2.51
Semantic > Visual	-63	-37	+2	3.56	<0.001 uncorr	N/A	<b>22</b>	<b>6.16**</b>	<b>2.17</b>

Table 4: Statistical details for hearing status and task interactions in right STC

	Deaf > Hearing						Deaf		Hearing	
	x	y	z	Z-score	p-value	k		Z-sc. relative to baseline		
						FWE	p<.001			
						corrected	uncorrected			
BSL Phonological task	+66	-34	+8	4.69	<0.001 uncorr	N/A	<b>150</b>	2.12	-4.73*	
Semantic task	+66	-34	+8	5.08	0.010 FWE	<b>3</b>	<b>67</b>	3.29*	-4.11*	
Visual task	+66	-34	+8	4.63	<0.001 uncorr	N/A	<b>37</b>	3.49*	-3.18*	
BSL Phonological > Semantic	+69	-28	-1	3.70	<0.001 uncorr	N/A	<b>12</b>	4.71*	-0.08	
BSL Phonological > Visual	+60	-31	+2	3.99	<0.001 uncorr	N/A	<b>20</b>	3.22*	-2.46	
Semantic > Visual	+60	-28	+2	3.39	<0.001 uncorr	N/A	<b>2</b>	2.24	-2.66	

Table 5: Statistical details for the regions in which activation was greater for deaf than hearing signers across all tasks at  $p < .05$  FWE corrected ( $Z > 4.76$ ).

Region	Deaf > Hearing			Z-score	p-value	k		Deaf Z-sc. > baseline	Hearing	
	x	y	z			(FWE corrected)	FWE			p < .001
							corrected			uncorrected
Temporal										
R Superior temporal gyrus	+66	-34	+8	5.35	0.002	6	86	3.27*	-4.55**	
Occipital										
R Lingual gyrus	+21	-85	-4	5.11	0.008	1	29	8.25**	6.54**	
R Middle occipital gyrus	+45	-79	-7	4.83	0.035	2	32	8.69**	8.08**	
L Middle occipital gyrus	-30	-85	+11	5.22	0.005	4	56	8.71**	8.03**	
L Fusiform gyrus	-33	-61	-7	5.05	0.011	1	21	8.04**	5.24**	
L Calcarine sulcus	-12	-94	+2	4.84	0.033	2	25	8.61**	7.92**	