1   **The role of the superior parietal lobule in lexical processing of sign language: Insights from**

2   **fMRI and TMS**

3

4   Banaszkiewicz A.[1], Bola Ł.[1], Matuszewski J.[1], Szczepanik M.[1], Kossowski B.[1], Mostowski P.[2],

5   Rutkowski P. [2], Śliwińska M. [3], Jednoróg K.[4], Emmorey K.[5], Marchewka A.[1*]

6

7   [1] Laboratory of Brain Imaging, Nencki Institute of Experimental Biology, Polish Academy of

8   Sciences, Warsaw, Poland;

9   [2] Section for Sign Linguistics, Faculty of Polish Studies, University of Warsaw, Warsaw, Poland

10   [3] Department of Psychology, University of York, Heslington, UK

11   [4] Laboratory of Language Neurobiology, Nencki Institute of Experimental Biology, Polish

12   Academy of Sciences, Warsaw, Poland

13   [5] Laboratory for Language and Cognitive Neuroscience, San Diego State University, San Diego,

14   USA

15

16

17

18

19

20

21

22

23

24

25

26   [*]Correspondence to:

27   Artur Marchewka, PhD

28   Laboratory of Brain Imaging (LOBI)

29   Nencki Institute of Experimental Biology, Polish Academy of Sciences

30   Pasteur 3, 02-093 Warsaw, Poland

31   Email: a.marchewka@nencki.edu.pl

32   Phone: +48 22 5892 549; Fax: +48 22 5892 49

Highlights

- Activity of left, but not right, SPL changed with sign language learning
- Hearing learners showed more activation of bilateral LOC & left SPL than deaf signers
- TMS applied to the right SPL decreased accuracy in hearing learners and deaf signers
- TMS applied to the left SPL decreased accuracy only in hearing learners
- R SPL may be involved in visuospatial attention & L SPL in form decoding in learners

Abstract

There is strong evidence that neuronal bases for language processing are remarkably similar for sign and spoken languages. However, as meanings and linguistic structures of sign languages are coded in movement and space and decoded through vision, differences are also present, predominantly in occipitotemporal and parietal areas, such as superior parietal lobule (SPL). Whether the involvement of SPL reflects domain-general visuospatial attention or processes specific to sign language comprehension remains an open question. Here we conducted two experiments to investigate the role of SPL and the laterality of its engagement in sign language lexical processing. First, using unique longitudinal and between-group designs we mapped brain responses to sign language in hearing late learners and deaf signers. Second, using transcranial magnetic stimulation (TMS) in both groups we tested the behavioural relevance of SPL's engagement and its lateralisation during sign language comprehension. SPL activation in hearing participants was observed in the right hemisphere before and bilaterally after the sign language course. Additionally, after the course hearing learners exhibited greater activation in the occipital cortex and left SPL than deaf signers. TMS applied to the right SPL decreased accuracy in both hearing learners and deaf signers. Stimulation of the left SPL decreased accuracy only in hearing learners. Our results suggest that right SPL might be involved in visuospatial attention while left SPL might support phonological decoding of signs in non-proficient signers.

Introduction

Research on sign languages has provided new perspectives into the nature of human languages. Although they fundamentally differ from speech with respect to perceptual and articulatory systems required for production and comprehension, striking parallels are also present – including both formal linguistic aspects as well as overlapping neural substrates (Emmorey, 2002; Poeppel et al., 2012). A number of previous functional magnetic resonance imaging (fMRI) studies (i.e. Emmorey et al., 2014; MacSweeney et al., 2004; 2006; 2008a) have provided strong evidence that fundamental bases for language processing are remarkably similar for sign and spoken language. For example, sign language comprehension engages the left-lateralized perisilvian network. These areas – inferior frontal gyrus (IFG), superior temporal gyrus (STG) and inferior parietal lobule (including supramarginal and angular gyri), have been therefore highlighted as a universal, largely independent of the modality, language processing core. Despite the extensive overlap between brain networks supporting sign and speech processing, key differences are also present. Sign languages convey linguistic information through visuospatial properties and movement, which is reflected in the greater activity within modality-dependent neural systems located predominantly in occipitotemporal (e.g. inferior/middle temporal and occipital gyri; ITG, MTG) and parietal regions, such as superior parietal lobule (SPL). All together, these patterns of neural activity have been consistently observed in native signers – both deaf and hearing (who acquired sign language in early childhood; Corina et al., 2007; Emmorey et al., 2014; Jednoróg et al., 2015; MacSweeney et al., 2002; 2004; 2006; Newman et al., 2015; Sakai et al., 2005) as well as hearing late learners (Johnson et al., 2018; Williams et al., 2016).

However, it remains uncertain whether the involvement of modality-dependent regions is linguistically relevant or rather exclusively linked to bottom-up perceptual mechanisms. Here we focus on the functional involvement of the parietal cortex – in particular, the SPL – during sign language processing. The unique engagement of SPL in processing of sign language has been reported in several studies of both sign production (e.g., Emmorey et al., 2007; Emmorey et al., 2016) and sign comprehension (e.g., Braun et al., 2001; Emmorey et al., 2014; McCullough et al., 2012; MacSweeney et al., 2002b). SPL is hypothesized to play an important role in the analysis of spatial elements (e.g., locations on the body or in space) that carry linguistic meaning in sign languages (see Corina et al., 2006; MacSweeney et al., 2008a, and MacSweeney & Emmorey, 2020, for reviews). However, SPL has been also associated with

92   non-linguistic functions related to processing movement in space (Grefkes et al., 2004) or
93   understanding of human manual actions, such as grasping, reaching and tool-use (see Creem-
94   Regehr, 2009, for review). Thus, whether its involvement has an essential domain-specific
95   contribution to sign language comprehension is still an open question.

96   Along the same line, whether SPL activation during sign language processing is dependent on
97   proficiency or age of acquisition remains elusive. Some evidence about the characteristics of
98   SPL involvement in sign language comes from studies on hearing adult participants learning
99   to sign. In the longitudinal fMRI study of Williams et al. (2016), participants performed a
100   phonological task. At pre-exposure, sign-naïve individuals activated left SPL while analyzing
101   unknown signs only at the sensory, visuomotor level. At later learning stages, the transition to
102   phonological processing occurred and was reflected in the subsequent recruitment of
103   language-related areas and enhanced recruitment of the occipitotemporal and parietal
104   regions, including bilateral SPL (Williams et al., 2016). Nevertheless, direct contrasts between
105   first and subsequent time points did not reveal any significant difference in the strength of SPL
106   activation. Similarly, a cross-sectional study by Johnson and colleagues (2018) showed that
107   when acquired late in life and at a basic level of proficiency, sign language activated bilateral
108   SPL in hearing learners performing lexical and sentential tasks. However, with respect to
109   laterality of SPL engagement in sign language comprehension, earlier research with deaf and
110   hearing native signers provided mixed reports. Among these studies some reported only left-
111   hemisphere (MacSweeney et al., 2002, 2004), only right-hemisphere (Corina et al., 2007) or
112   bilateral activation (Emmorey et al., 2014; Conder et al., 2017; Emmorey et al., 2002; 2005;
113   MacSweeney et al., 2002a; 2008a).

114   Here we conducted two experiments to investigate the role of SPL in sign language
115   comprehension. First, using a longitudinal fMRI study design we explored the pattern of neural
116   changes throughout the course of sign language acquisition in hearing learners (HL).
117   Subsequently, to uncover the potential influences of age of acquisition and proficiency on SPL
118   involvement in sign language, we compared brain activation of deaf signers and HL, when the
119   latter were still naïve to sign language (before the sign language course) and 8 months later
120   at the peak of their skills (after the sign language course). Second, using transcranial magnetic
121   stimulation (TMS) we tested in both deaf signers and HL after the course whether SPL

122 engagement is behaviorally relevant for sign language comprehension, and if there are
123 hemispheric differences.

124 If SPL involvement in sign language reflects only the low-level spatial properties of sign
125 language itself, while not being linguistically relevant then we should observe brain activation
126 in SPL in deaf signers as well as HL before and after the course. Furthermore, no changes in
127 the level of activity in HL over learning time would be observed. If however SPL activity is
128 involved in sign language comprehension, then we should observe a significant change in its
129 recruitment resulting from sign language acquisition. Considering findings in spoken
130 languages (see Abutalebi, 2008; Stowe & Sabourin, 2005; van Heuven & Dijkstra, 2010, for
131 review) we also predicted that HL after the course would display a higher level of activation
132 than deaf signers, related to the lower level of automatization and greater requirement of
133 cognitive resources. Finally, we expected TMS administered to the SPL to hinder performance
134 in both hearing and deaf participants, with possible hemispheric differences related to each
135 group's different proficiency in sign language.

136

137 **Materials and methods**

138

139 No part of the study procedures or analyses was pre-registered prior to the research being
140 conducted. We report how we determined our sample size, all data exclusions, all
141 inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to
142 data analysis, all manipulations, and all measures in the study.

143

144 **EXPERIMENT 1 – fMRI**

145 **Participants**

146 　　　　Thirty-three hearing females were recruited to participate in the study. Ten
147 participants dropped out of the study due to personal or medical reasons. Three participants
148 were excluded from the analysis due to technical problems with registration of their
149 responses. Therefore, data from 20 participants were included in the fMRI analysis (mean age
150 at pre-exposure = 23.0, SD = 1.4, range = 20.3 – 25.7). Those participants come from a larger
151 longitudinal MRI study on sign language acquisition. Sample size and gender were matched
152 with another (all female) group for a separate study of tactile Braille alphabet and spoken

language (Greek). In addition, sample size of hearing participants was also determined having
in consideration participants' comfort and suitable learning environment during PJM lessons.
The participants reported Polish as their first language and were naïve to Polish Sign Language
(polski język migowy – PJM) prior to enrolment in the study.

Twenty-one deaf females were also recruited to participate in the experiment. We
aimed to match the sample size of hearing and deaf groups. One participant was excluded
from the analysis due to technical problems with registration of responses, and one
participant was excluded due to scoring below the age norms on the Raven Progressive
Matrices test. Six participants dropped out of the study due to personal or medical reasons.
Therefore, 13 deaf participants were included in the fMRI analysis (mean age = 27.7, SD = 4.1,
range = 19.8 – 34.8). Similar sample size of deaf participants was reported in previous studies
targeting brain activity in deaf population in response to sing language (Emmorey et al., 2010,
N =14; Jednoróg et al., 2015, N = 15; McCullough et al., 2012, N = 12). All of the deaf
participants were born into deaf, signing families and reported PJM as their first language.
Twelve individuals were congenitally deaf; one person reported hearing loss at the age of
three. The mean hearing level, as determined by audiogram data, was 93.3 dB for the right
ear (range = 70 – 120 dB) and 96.9 dB for the left ear (range = 80 – 120 dB). The majority of
deaf participants were using hearing aids (N = 8) and their speech comprehension with the aid
varied from poor to very good (see Table S1 for details). They were assisted by a PJM
interpreter during the whole study.

All participants included in the final analyses were right-handed, healthy, had normal
or corrected-to-normal vision and nonverbal IQ (Raven Progressive Matrices) within the age
norms. They had 13 or more years of formal education (one hearing and four deaf participants
completed higher education). Both hearing and deaf participants had no contraindications to
the MRI, gave written informed consent and were paid for participation. The study was
approved by the Committee for Research Ethics of the Institute of Psychology of the
Jagiellonian University.

Polish Sign Language course and behavioral measurements

Participants underwent a PJM course specifically designed for the purpose of this study. The
course was executed and accredited by a PJM school – EduPJM (http://edupjm.pl/) and run
by two certified teachers of PJM, who were deaf native signers. The classes were 1.5 hours

184 long and took place twice a week [57 meetings, 86 hours, M = 73.5 hours of instruction (range

185 = 45.0 – 84.0, SD = 9.9), due to absences]. The program of the course provided an increasing

186 complexity of applied themes and activities. At the end, learners reached A1/A2 proficiency

187 level, being able to describe immediate environment and matters, hold a conversation or

188 comprehend a simple monologue.

189

190 **Tasks and stimuli**

191 Hearing participants underwent five fMRI sessions performed in the ~2.5-month

192 intervals: Time Points TP0-TP4, where TP0 was a pre-exposure scan, TP3 was a scan at the end

193 of the course, and TP4 a follow-up scan. Deaf signers participated in one fMRI session that was

194 matched in time to TP3 (Figure 2A).

195 The experimental task was based on lexical processing (Lexical Decision Task; LDT;

196 Binder et al., 2009), presented in two conditions – Explicit (EXP), requiring a linguistic decision,

197 and Implicit (IMP), involving gender discrimination (no explicit linguistic decision was required,

198 but implicit language processing could occur). In order to control for nonspecific repetition

199 effects, HL performed an additional control task of reading in L1 (Polish) that was implemented

200 at each TP. Our assumption was that a lack of differences between time points in L1 would

201 provide strong evidence that functional changes observed in L2 were indeed training-specific

202 and not a consequence of task repetition.

203 PJM task: LDT EXP required a lexical decision about whether a presented stimulus was

204 an existing sign (e.g., FRIEND) or a pseudosign (a non-meaningful, but possible PJM sign

205 created by changing at least one phonological parameter of an existing sign, such as

206 movement, handshape, location or orientation; Emmorey et al., 2011). For the IMP condition,

207 stimuli of the same type were presented, however, participants were asked to indicate the

208 gender of the sign model for each stimulus.

209 Sign stimuli were verbs, nouns and adjectives, covering a wide range of everyday

210 categories. For each TP, signs were adjusted to match participants' skills – only those that had

211 already been learned were included. The task difficulty was balanced across TPs: at each

212 session the presented stimuli were derived from all signs learned prior to that TP, so at TP1

213 they included signs learned during the first 3 months, while the stimuli presented at TP2 and

214 TP3 consisted of signs acquired not only in the last learning period, but also earlier during the

215 course. Stimuli presented at TP0 and TP4 were also taken from all learning periods, but were

216 different from those presented at TP3. Since at TP0 participants were naïve to PJM, stimuli

217 presented at TP4 were identical (however, the stimuli were presented in a different order).

218 Stimuli presented to deaf signers were those used at TP3.

219   In total, 320 video clips were recorded by native Deaf signers (one female and one

220 male), dressed in black t-shirts and standing in front of a grey screen, with full-face and torso

221 exposed. They were asked not to produce large mouth movements ("mouthings") that are

222 closely associated with a Polish translation of a sign, in order to avoid lip reading. Videos were

223 displayed using Presentation software (Neurobehavioral Systems, Berkeley, CA) on a screen

224 located in the back of the scanner, reflected in the mirror mounted on the MRI head coil.

225 Sample stimuli are listed in Table S2, and the experimental material are available at:

226 https://osf.io/bgjsq/

227   Polish L1 control task: in the LDT condition HL were asked to discriminate written

228 words (e.g. "BANANA") and pseudowords (e.g. "BAPANA"). In the visual search condition,

229 random letter strings were displayed on the screen. Half of the strings contained two "#" (e.g.

230 KB#T#) and half did not (URCJW), and participants were asked to to discriminate both types

231 of letter strings.

Procedure

233   The PJM and Polish L1 tasks were presented in separate runs, in a mixed block/event

234 design. The PJM EXP and IMP conditions were presented alternately and counterbalanced

235 across participants. The task consisted of 5 EXP and 5 IMP blocks with 8 (4 signs/pseudosigns

236 or words/pseudowords) pseudorandomized trials per block. Before each block, a fixation cross

237 was presented for 6 – 8 seconds, followed by 2 seconds of a visual cue informing participants

238 about the type of incoming block (EXP or IMP) followed by another fixation cross (1 – 2

239 seconds). In PJM the total duration of LDT was on average 8.1 min (mean block duration = 43

240 s; mean stimuli length = 2.2 sec; answer window: 2 sec; Inter Stimulus Interval (ISI): 1 sec. The

241 total duration of the Polish control task was 6.5 min (block duration = 32 sec.; stimuli length =

242 1 sec; answer window = 2 sec; ISI = 1 sec).

243

Imaging parameters

245   MRI data were acquired on a 3T Siemens Trio Tim MRI scanner using 12-channel head coil.

246 T1-weighted (T1-w) images were acquired with the following specifications: 176 slices, slice-

247 thickness = 1 mm, TR = 2530 ms, TE = 3.32 ms, flip angle = 7 deg, FOV = 256 mm, matrix size:

248 256 × 256, voxel size: 1x1x1 mm. An echo planar imaging (EPI) sequence was used for

249 functional imaging. Forty-one slices were collected with the following protocol: slice-thickness

250 = 3 mm, TR = 2500, flip angle = 80 deg, FOV = 216 × 216 mm, matrix size: 72 × 72, voxel size: 3

251 × 3 × 3 mm).

252

253 **fMRI analyses**

254 The pre-processing and statistical analyses of fMRI scans were performed using SPM12

255 (Wellcome Imaging Department, University College, London, UK, http://fil.ion.ucl.ac.uk/spm),

256 run in MATLAB R2013b (The MathWorks Inc. Natick, MA, USA). First, if needed, structural and

257 functional images were manually reoriented to origin in Anterior Commissure. Next,

258 functional volumes acquired at all TPs were together realigned to the first scan and motion

259 corrected. Then, in the case of hearing participants, the structural longitudinal registration

260 SPM toolbox was used to create average T1-weighted image from five scans, to assure an

261 identical normalization procedure over time. Functional images were normalized to MNI

262 (Montreal Neurological Institute) space using deformation fields acquired from T1-w

263 (averaged in case of hearing participants), co-registered to mean functional image. Finally,

264 normalized images were smoothed with 6 mm full width at half maximum Gaussian kernel.

265 Statistical analysis was performed on participant (1st) and group (2nd) levels using

266 General Linear Models. At the 1st level, onsets of correct and incorrect trials in the EXP and

267 IMP condition as well as onsets of missing responses were entered into design matrices with

268 the addition of six head movement regressors of no interest. Obtained functions were then

269 convolved with the hemodynamic response function as implemented in SPM12. Data were

270 filtered with 1/160 Hz high-pass filter, adjusted to the duration of LDT block (mean = 43 sec).

271 At the 2nd level, a set of analysis was performed for HL pre- and post-training and deaf signers.

272 Beta estimates of correct trials in the EXP condition were used to compute statistical models.

273 First, using one-sample t-tests, the LDT was investigated in each group. Then, two-sample t-

274 tests were performed to compare brain activity between hearing (at TP0 and TP3) and deaf

275 participants. Next, EXP and IMP conditions from TP3 were entered into a flexible factorial

276 model, with 2 (group: HL and deaf) x 2 (condition: EXP and IMP) factors and additional subject

277 factor. Group factor was specified with unequal variance, condition and subject factors were

278 specified with equal variance. Then, a contrasts testing a group x condition interaction was

computed. In order to explore the pattern of neural changes in hearing participants between TP0 and TP4, the EXP and IMP conditions from all TPs were entered into a flexible factorial model, with 5 (time point) x 2 (condition: EXP and IMP) factors – both specified with unequal variance – and subject factor, specified with equal variance and a contrast testing the main effect of time was computed. Finally, post-hoc pairwise comparisons between consecutive time points in EXP condition were performed (TP0 vs. TP1, TP1 vs. TP2, TP2 vs. TP3 and TP3 vs. TP4; the results can be found in supplementary materials 1.1., Figure S1 and Table S4).

Polish L1 control task: At the 1st level, task and time point-specific timings of all conditions together with six head movement regressors were entered in the model. At the 2nd level, a one-way within subject ANOVA 5 (time point) x 1 (LDT condition) model was computed using a mask of task positive activations from the experimental (PJM) and control conditions (Brennan et al., 2013).

In the main effect of time analysis task-related responses were considered significant at $p < 0.05$, using a voxel-level Family Wise Error correction (FWE). An additional extent threshold of > 20 voxels was applied. In the rest of the models task-related responses were considered significant at $p < 0.05$, using cluster-level FWE correction (FWEc). Anatomical structures were identified with the probabilistic Harvard-Oxford Atlas (http://www.cma.mgh.harvard.edu/) for cortical and subcortical areas and the AAL atlas (Tzourio-Mazoyer et al., 2002) for cerebellar areas. Finally, to illustrate the pattern of activity changes over time, as well as the interaction between group and condition in left and right SPL, independent, anatomically-instructed regions of interest (ROIs) were defined using the Harvard-Oxford Atlas.

EXPERIMENT 2 (TMS)

Participants

Eighteen hearing participants who underwent Experiment 1 also participated in the subsequent TMS study. Four individuals were excluded from the analysis due to incomplete data, problems with localizing target structures or reported discomfort during stimulation. Two participants, who were previously excluded from Experiment 1 due to technical issues, took part in the TMS study. Therefore, 14 hearing participants were included in the TMS analysis. Additionally, 13 deaf participants previously enrolled in Experiment 1 participated in

the TMS session, among whom one was previously excluded from fMRI analyses due to technical problems.

Both hearing and deaf participants had no contraindications to TMS, gave written informed consent and were paid for their participation. The experiment was approved by the Committee for Research Ethics of the Institute of Psychology of the Jagiellonian University.

Task and stimuli

Approximately six weeks after TP3 (hearing group: mean = 5.7 weeks, SD = 1.6, range = 4.6 – 10.7), a repetitive TMS (rTMS) experiment was conducted (Figure 2A). Hearing and deaf participants were instructed to watch sign language video clips and perform the LDT EXP task requiring discrimination between signs and pseudosigns. The stimuli were produced by the same native PJM models as from the fMRI experiment, with full-face and torso exposed, presented in short videos (~2 s. long; Figure 1A). Responses were collected using a Cedrus response pad RB-840 (https://cedrus.com/rb_series/). The response pad was placed in front of the participants who were sitting by the table. They were asked to press a button with their right hand using the index finger for one decision (sign) and middle finger for the other decision (pseudosign). In total, 480 video clips were used in the TMS study (240 signs and 240 pseudosigns).

Localization of TMS sites

During the experiment TMS was delivered to three target sites – right SPL (R SPL), left SPL (L SPL) and a control site – occipital pole (OP; Figure 1B). Both SPLs were marked on each participant's structural MRI scan. In the hearing group TMS delivery was based on individual structural MRI/fMRI data at TP3, using peaks of activation from the LDT EXP condition. The OP was localized anatomically for each participant and the coil was placed at the ~45 degrees angle, so that the center of the coil was not touching the skull. Three participants used MRI-compatible glasses during the fMRI session correcting for insufficient vision, which caused T1-w image artifacts. Therefore their target regions were localized on a standard MNI template. Since in the deaf group fMRI analysis did not reveal significant clusters of activation in bilateral SPL, all of the target regions were assessed based on anatomical landmarks in the native structural images (T1-w). To verify the accuracy of our localization procedure, single-subject coordinates for right and left SPL were normalized to the MNI space and averaged across

342 participants. The obtained mean MNI coordinates for the HL group were: x = -30 ± 9, y = -55

343 ± 8, z = 42 ± 8 (left SPL) and x = 33 ± 8, y = -55 ± 5, z = 44 ± 8 (right SPL) and for deaf group: x

344 = -30 ± 9, y = 59 ± 8, z = 56 ± 7 (left SPL) and x = 30 ± 7, y = -60 ± 7, z = 56 ± 5 (right SPL; see

345 Table S5 with MNI coordinates for individual participants).

346

347 **TMS protocol**

348 A MagPro X100 stimulator (MagVenture, Hückelhoven, Germany) with a 70 mm figure-

349 eight coil was used to apply the TMS. A neuronavigation system (Brainsight software, Rogue

350 Research, Montreal, Canada) was used with a Polaris Vicra infrared camera (Northern Digital,

351 Waterloo, Ontario, Canada) to guide stimulation.

352 Pulses were administered to each target site at 400, 600, 800, 1000 and 1200 ms post-

353 stimulus onset (5 Hz; Figure 1A). The first TMS pulse was administered 400 ms after the start

354 of the video because the onset of the sign or pseudosign occurred ~400 ms after video onset

355 which began with the model's hands at rest along the body. Intensity was set to 110% of the

356 individual motor threshold, measured by a visible twitch of the hand during single TMS pulses

357 administered to the hand area in the left primary motor cortex (average intensity = 40% of the

358 maximum stimulator output power; SD = 6%, range = 27-54%). Pulses were applied

359 pseudorandomly on half of the trials (TMS vs. no TMS conditions). There were three

360 experimental runs, one run per anatomical structure. The order of stimulated structures was

361 counterbalanced across participants.

362 **Procedure**

363 After participants provided informed consent and completed a safety screening

364 questionnaire, the structural MRI scan with the marked TMS target sites was co-registered to

365 the participant's head. Next, the resting motor threshold was measured. In order to familiarize

366 participants with the task and TMS protocol, two short training sessions were performed

367 without and with TMS. The actual TMS experiment was subsequently conducted. Each run

368 started with a fixation cross (15 sec) and consisted of 160 stimuli, counterbalanced between

369 TMS and no TMS conditions (that is, a given sign was in the TMS condition for half of

370 participants, and in the no TMS condition for the other half). Trials were followed by a fixation

371 cross displayed for 3-5 sec. and response time was counted from the stimulus onset until 1

372 sec. after its end (Figure 1A). Participants responded using a dedicated response pad. During

373 each run participants were provided with two short breaks. In total the duration of

374 experimental runs was ~20 min. Each run was followed by a break lasting a few minutes.
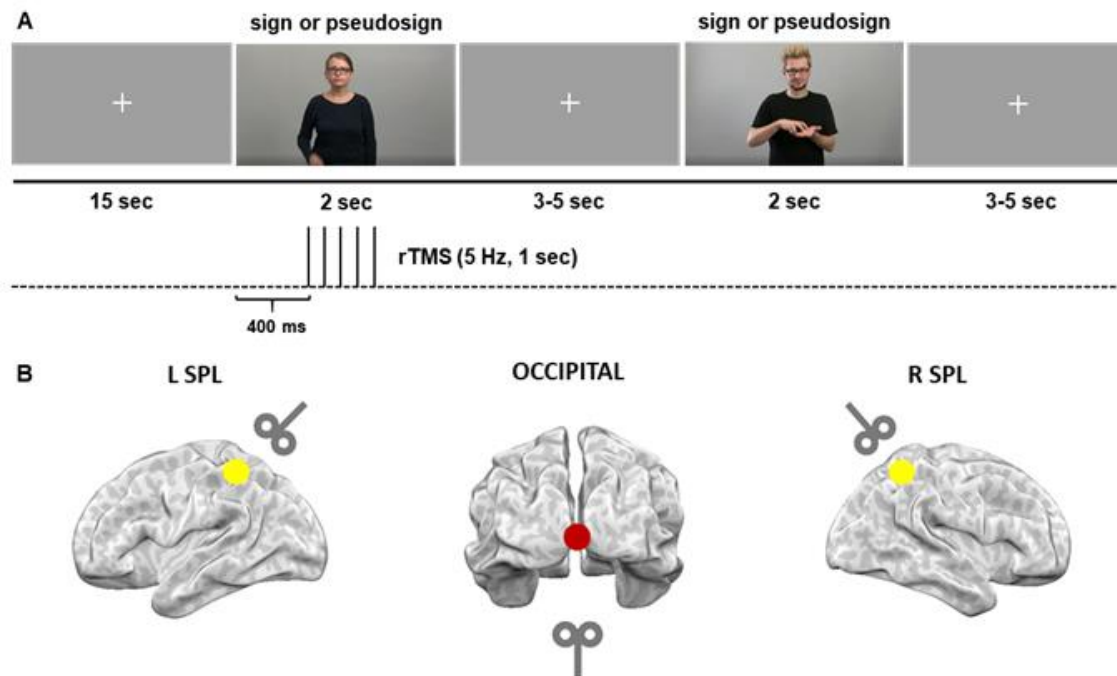
375

376

377 Figure 1. Experimental design of the TMS study. A) Hearing and deaf participants performed a

378 lexical task in sign language, requiring discrimination between signs and pseudosigns. Each

379 run started with a fixation cross (15 sec). The stimuli were ~2 sec long and were followed by a

380 fixation cross displayed for 3-5 sec. Response time was counted from the stimulus onset until

381 1 sec after its end. Pulses were administered at 400, 600, 800, 1000 and 1200 ms post-stimulus

382 onset (5 Hz). B) TMS was delivered to three target sites – right SPL, left SPL and a control site

383 – the occipital pole at 110% of the individual motor threshold.

384 **Results**

385 **EXPERIMENT 1 – fMRI**

386 **Behavioral results**

387   Two-sample t-tests were performed in order to explore the differences in the accuracy

388 in LDT between hearing and deaf participants. First, HL before the course were compared to

389 the deaf signers. This comparison revealed that the deaf group performed significantly better

390 [$t(31) = 7.69$; $p < 0.001$]. The comparison between HL post-training and deaf signers showed

391 no significant differences between the groups ($p = 0.45$). Additionally, the comparison

392 between performance of HL before and after the course using paired t-tests revealed an
393 improvement at the end of the course of PJM, reflected in a significantly higher accuracy for
394 post-training than pre-training [t(19) = 11.65; p < 0.001; Figure 2B]. Details about participants'
395 scores can be found in Table S3).
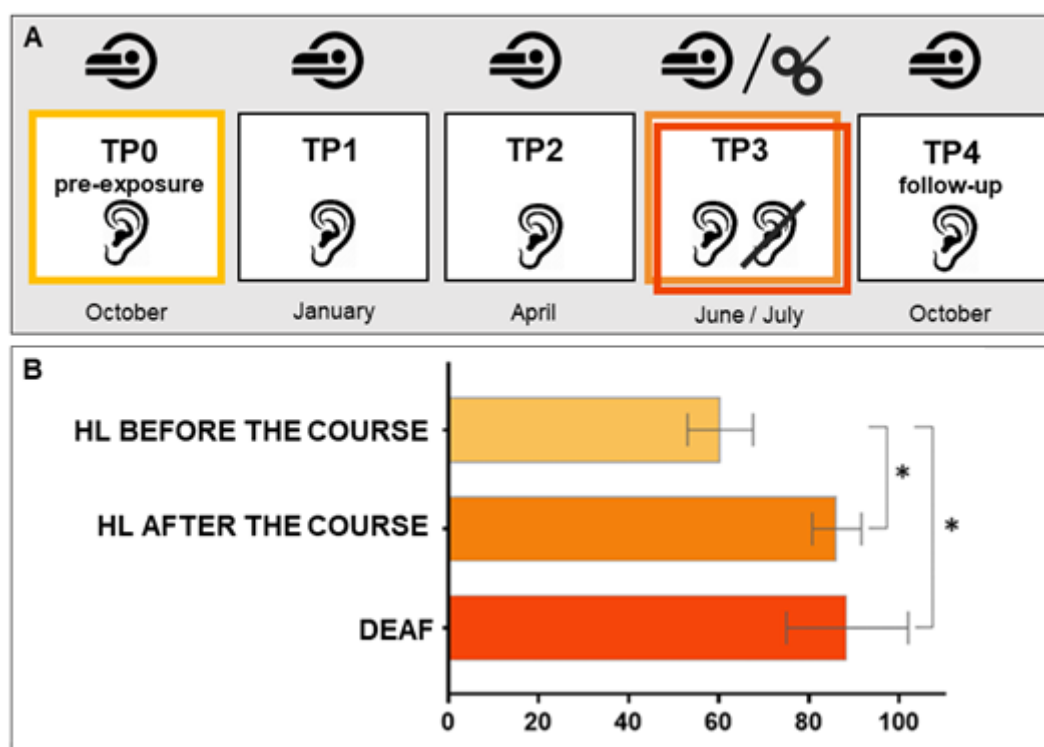
396

397
398

399 Figure 2. A) Hearing participants underwent five fMRI sessions performed in the ~2.5-month
400 intervals: Time Points TP0-TP4, where TP0 was a pre-exposure scan, TP3 was a scan at the end
401 of the course and TP4 a follow-up). Deaf signers participated only in a single fMRI session that
402 was matched in time to TP3. Approximately six weeks after TP3 hearing and deaf participants
403 underwent the TMS session. B) Behavioral results for the sign language lexical decision task.
404 Differences in accuracy scores for hearing learners (HL) before and after the course and
405 between HL and deaf participants are indicated with an asterisk. *p ≤ 0.001; error bars
406 represent SD.

407

408 **fMRI results**

409 **PJM processing in hearing learners before the course**

410 The LDT performed by hearing participants at pre-exposure, resulted in activation in
411 the right, but not in the left SPL. Bilateral activation was also observed in IFG pars opercularis,

412   precentral gyrus (PreCG), postcentral gyrus and supramarginal gyrus (SMG). Furthermore,

413   significant clusters were observed in bilateral MTG and the superior part of lateral occipital

414   cortex (LOC). Additionally, subcortical regions such as thalamus and putamen were engaged

415   bilaterally (see Figure 3B and Table 1).

416

417   **PJM processing in hearing learners after the course and in deaf signers**

418   One sample t-tests revealed that HL and deaf signers activated prefrontal regions,

419   including bilateral IFG and PreCG, together with occipitotemporal areas of MTG and LOC.

420   Additionally, both groups activated SMG as well as subcortical regions such as thalamus and

421   putamen. In addition, deaf signers recruited bilateral STG. Post-training, the HL participants

422   recruited bilateral SPL, whereas no activation in these regions was observed in the deaf

423   participants (see Figure 3B-C and Table 1).

424

425   **Main effect of time point in hearing learners**

426   Over the course of PJM learning, brain activation in hearing individuals during LDT

427   changed in left hemisphere cortical regions – PreCG, IFG and SMG as well as SPL. No significant

428   changes in activation over time were observed in the right SPL. Additional significant clusters

429   were found in bilateral LOC and Fusiform Cortex (Figure 3D and Table 1). For more detailed

430   results and discussion of above analysis see supplementary materials 1.2. Finally, pairwise

431   comparisons between consecutive time points revealed significant activation increases at TP1

432   > TP0 in bilateral LOC extending to SPL in the left hemisphere as well as left PreCG and IFG

433   (see supplementary materials 1.1., Figure S1 and Table S4). An analogous contrast exploring

434   the main effect of time in the control task of reading in L1 did not reveal any significant
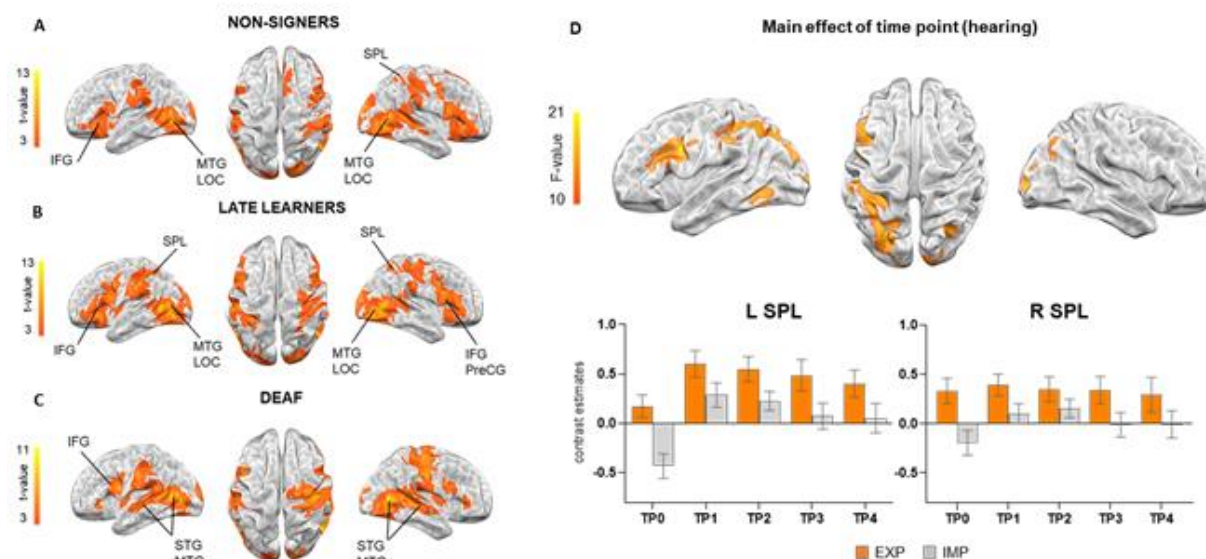
435   clusters.

436

Figure 3. A-C) Brain activations during lexical processing of sign language for each group ($p <$ 0.05; FWEc). D) Results from the main effect of time point in hearing learners ($p < 0.05$; FWE); bar graphs of independently defined ROIs are shown to illustrate the time course of changes. Error bars represent SEM. EXP: explicit condition; IMP: implicit condition (gender discrimination).

Differences in PJM processing between groups

Two sample t-tests with the contrasts deaf > HL before the course and deaf > HL after the course revealed greater activation in bilateral planum temporale and STG in both comparisons. The contrast HL before the course > deaf revealed only one cluster in the left MFG. The HL after the course > deaf comparison showed greater activity in the bilateral LOC and left SPL (see Figure 4 and Table 1).
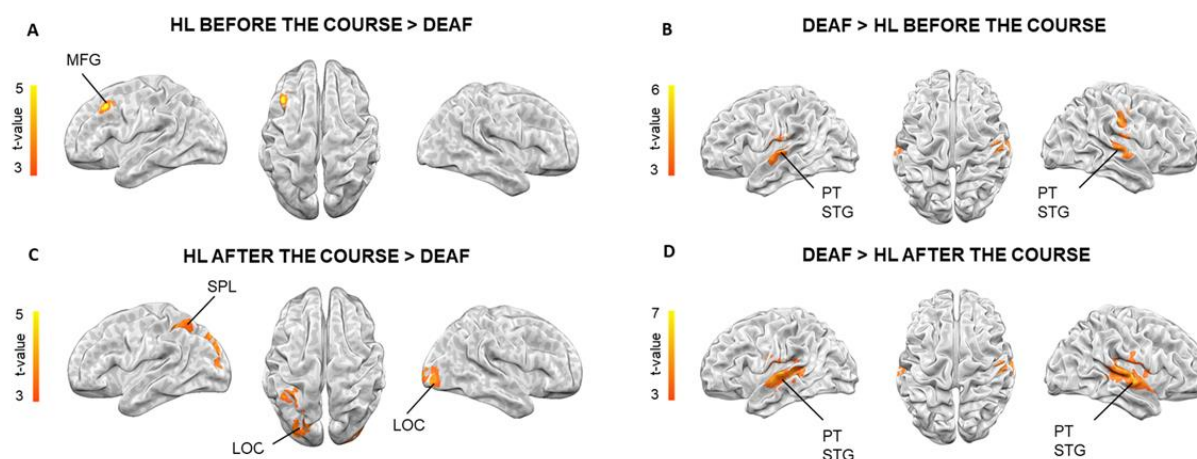
457

458

459 Figure 4. Brain activation differences during lexical processing of sign language between

460 groups at $p < 0.05$; FWEc.

461

462 **Table 1.** Results from one-sample t-test for each group and main effect of time in hearing

463 learners.

464

Brain regions	Cluster size	t-value	MNI Coordinates		
			x	y	z
HL before the course					
Left hemisphere					
Lateral Occipital Cortex (inferior)	1957	11,3	-46	-68	4
Temporal Occipital Fusiform Cortex		7,8	-42	-50	-18
Middle Temporal Gyrus (temporooccipital)		7,3	-52	-58	0
Inferior Frontal Gyrus (opercularis)	1768	7,0	-52	10	8
Postcentral Gyrus	906	7,4	-58	-20	26
Superior Parietal Lobule	134	5,0	-30	-50	58
Right hemisphere					
Lateral Occipital Cortex (inferior)	8594	17,3	48	-66	2
Postcentral Gyrus		10,3	62	-18	38
Temporal Occipital Fusiform Cortex		9,6	40	-56	-20
Paracingulate Gyrus	878	6,8	4	20	44
Frontal Pole		4,8	8	44	50
Brain-Stem	349	6,4	4	-26	-2
Thalamus		5,5	10	-12	2

Region					
Putamen	182	5,8	20	6	6

HL after the course

Left hemisphere

Region					
Inferior Frontal Gyrus (opercularis)	2597	10,4	-48	10	28
Frontal Pole		9,1	-44	36	-2
Postcentral Gyrus	1554	7,7	-58	-18	28
Supramarginal Gyrus (anterior)		7,7	-54	-28	34
Left Thalamus	1384	8,9	-18	-30	-2
Insular Cortex	123	7,3	-38	-4	14

Right hemisphere

Region					
Lateral Occipital Cortex (inferior)	11262	17,2	46	-62	0
Occipital Pole		13,9	18	-98	6
Inferior Frontal Gyrus (triangularis)	2411	9,8	56	34	16
Precentral Gyrus		9,4	60	12	28
Right Thalamus	1384	8,4	8	-14	2
Paracingulate Gyrus	232	5,1	4	18	48

Deaf

Left hemisphere

Region					
Supramarginal Gyrus (anterior)	2506	12,9	-54	-30	36
Lateral Occipital Cortex (inferior)		10,5	-46	-64	10
Inferior Frontal Gyrus (opercularis)	662	9,2	-52	10	20
Occipital Pole	657	14,3	-10	-100	-2
Occipital Fusiform Gyrus		5,8	-14	-82	-10
Amygdala	249	10,2	-22	-6	-12
Inferior Frontal Gyrus (triangularis)	80	5,5	-50	28	-2
Frontal Orbital Cortex		4,7	-52	22	-8
Frontal Operculum Cortex		4,1	-38	26	0

Right hemisphere

Region					
Lateral Occipital Cortex (inferior)	5279	11,9	52	-66	2
Postcentral Gyrus	1886	10,4	50	-18	42
Putamen	800	9,4	30	-2	-4
Precentral Gyrus	347	9,5	54	10	14
Supplementary Motor Cortex	110	7,3	6	6	68
Superior Frontal Gyrus		4,9	6	20	68
Central Opercular Cortex	94	7,7	38	0	14
Inferior Frontal Gyrus (triangularis)	92	6,4	52	34	6
Frontal Orbital Cortex		5,3	42	28	-2
Inferior Frontal Gyrus (opercularis)		5,1	54	16	2

Main effect of time point – HL	Cluster size	F-value	x	y	z
Left hemisphere					
Lateral Occipital Cortex (superior)	1021	18,7	-28	-70	28
Superior Parietal Lobule		16,6	-32	-56	46
Supramarginal Gyrus (anterior)		15,6	-50	-30	38
Precentral Gyrus	521	21,3	-42	4	32
Inferior Frontal Gyrus (triangularis)		14,2	-40	26	20
Temporal Occipital Fusiform Cortex	175	15,5	-44	-56	-16
Right hemisphere					
Occipital Fusiform Gyrus	144	15,5	18	-76	-10
Lateral Occipital Cortex (superior)	128	16,6	32	-66	32
Precuneous	45	14,9	20	-56	22
Occipital Pole	42	13,0	12	-96	18

465

466

467

468

469

470

471

472

473

474

475

476

477

478

479

480

481

482

483 **Table 2.** Results from two-sample t-tests showing differences during lexical processing of sign
484 language between groups.

Brain regions	Cluster size	t-value	MNI Coordinates		
			x	y	z
HL before the course > deaf					
Left hemisphere					
Middle Frontal Gyrus	138	5,0	-42	18	38
Deaf > HL before the course					
Left hemisphere					
Central Opercular Cortex	260	5,2	-56	-14	18
Superior Temporal Gyrus (anterior)		4,9	-62	-10	-2
Cerebelum VI	129	4,0	-20	-54	-20
Right hemisphere					
Superior Temporal Gyrus (posterior)	188	4,9	66	-20	4
Planum Temporale		4,5	58	-24	8
Postcentral Gyrus	135	4,9	52	-16	38
HL after the course > deaf					
Left hemisphere					
Lateral Occipital Cortex (superior)	211	5,0	-30	-84	32
Superior Parietal Lobule	152	4,8	-42	-46	52
Lateral Occipital Cortex (superior)		3,9	-28	-60	48
Right hemisphere					
Lateral Occipital Cortex (inferior)	132	4,5	38	-88	-4
Deaf > HL after the course					
Left hemisphere					
Planum Temporale	889	5,8	-60	-18	4
Temporal Occipital Fusiform Cortex	219	3,9	-24	-62	-20
Right hemisphere					
Planum Temporale	1246	6,7	60	-22	8
Superior Temporal Gyrus (posterior)		6,4	66	-10	2
Lingual Gyrus	219	5,0	4	-76	-16
Temporal Pole	226	4,5	30	6	-20
Right Amygdala	128	4,1	32	6	-20

485 Lastly, a significant interaction between group and condition was revealed in the left SPL ($p <$

486 0.05, FWEc) and left insula. Subsequently, ROI analysis of the left SPL (derived independently

487 from Harvard-Oxford atlas) using mixed 2 (group) x 2 (condition) rmANOVA revealed a

488 significant main effect of group group [$F(1, 31) = 6.95$, $p < 0.05$, eta-squared = 0.18] and an

489 interaction between group and condition [$F(1, 31) = 6.64$, $p < 0.05$, eta-squared = 0.18]. Post

490 hoc t-tests showed that activity of the left SPL was significantly greater in the HL than in the

491 deaf group only in the EXP condition and significantly greater during EXP than IMP condition

492 in HL group (Figure 5.).

493
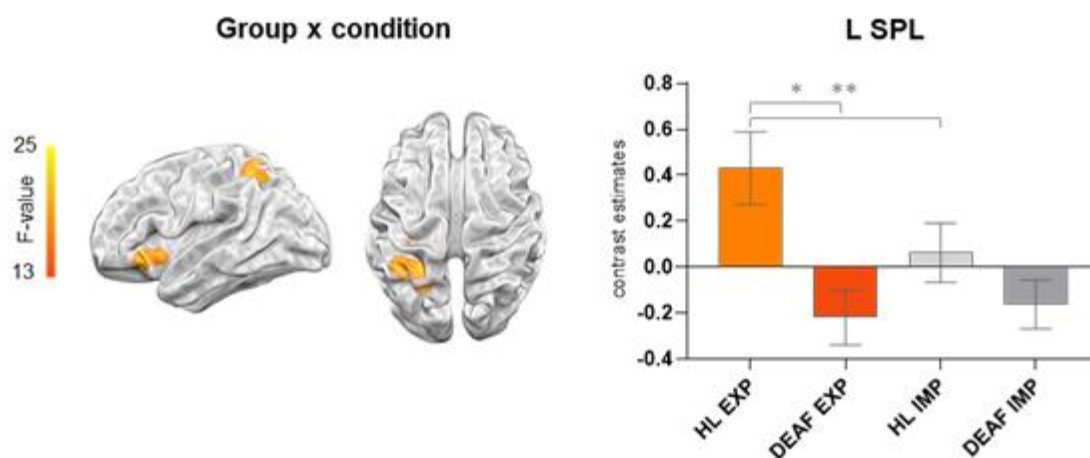
494 Figure 5. Whole-brain interaction of group (HL and deaf) by condition (EXP and IMP) at TP3 at

495 $p < 0.05$; FWEc; bar graphs of the independently defined ROI in the left SPL are shown to

496 illustrate the obtained interaction, *$p < 0.005$, ** $p = 0.001$, Bonferroni corrected. Error bars

497 represent SEM.

498 **EXPERIMENT 2 – TMS**

499 The three-way mixed analysis of variance (ANOVA) with structure (left SPL, right SPL

500 and OP), group (hearing learners/deaf signers) and condition (TMS/no TMS) as factors was

501 computed. The results showed a significant main effect of group [$F(1, 25) = 147.54$, $p < 0.001$,

502 eta-squared = 0.86], condition [$F(1, 25) = 18.09$, $p < 0.001$, eta-squared = 0.42] as well as

503 interactions: condition x structure [$F(2, 50) = 3.28$, $p < 0.05$, eta-squared = 0.12] and group x

504 structure x condition [$F(2, 50) = 3.99$, $p < 0.05$, eta-squared = 0.14]. Subsequently, three two-

505 way ANOVA models were computed for each structure separately (left SPL, right SPL and OP)

506 with group (hearing learners/deaf signers) and condition (TMS/no TMS) as factors. This

507 analysis indicated a significant main effect of group for the left SPL [$F_{(1, 25)} = 82.51$, $p < 0.001$,

508 eta-squared = 0.77], right SPL [$F_{(1, 25)} = 77.47$, $p < 0.001$, eta-squared = 0.76] and OP [$F_{(1,}$

509 $_{25)} = 60.41$, $p < 0.001$, eta-squared = 0.71], a main effect of condition for the left SPL [$F_{(1, 25)}$

510 = 5.04, $p < 0.05$, eta-squared = 0.17] and right SPL [$F_{(1, 25)} = 22.59$, $p < 0.001$, eta-squared =

511 0.46], as well as a significant interaction between condition and group for the OP [$F_{(1, 25)} =$

512 6.79, $p < 0.05$, eta-squared = 0.21]. Since we were particularly interested if similar effects are

513 found in both hearing and deaf participants we tested the effect of condition in both groups.

514 TMS delivered to the right SPL resulted in a decrease of accuracy in LDT in both hearing ($p \leq$

515 0.001) and deaf ($p < 0.05$) participants. For left SPL the TMS stimulation negatively affected

516 the performance only in the hearing group ($p < 0.05$). There was no significant TMS effect in

517 the control structure (OP) in either group (see Figure 6). Details about participants' scores can
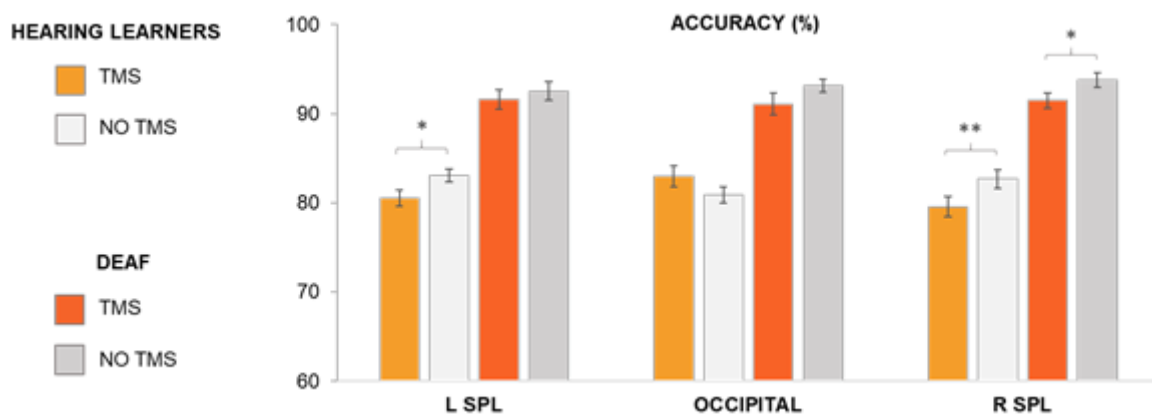
518 be found in Table S3.

519

522 Figure 6. Accuracy results from the TMS experiment: percentage of correct responses in the

523 Lexical Decision Task in hearing learners (after the course) and deaf signers during TMS/no

524 TMS conditions, *$p \leq 0.05$; **$p \leq 0.001$, Bonferroni corrected. For brevity, only differences

525 between TMS and no TMS conditions are indicated. Error bars represent SEM.

526

Discussion

528 In the current study, we sought to investigate the role of SPL in sign language comprehension.

529 We asked how sign language learning changes the pattern of SPL response to PJM signs in

530 hearing late learners and what are the differences between hearing individuals (prior to and

531 after the sign language course) and deaf individuals in SPL engagement during sign language

532 comprehension. Therefore, in the first fMRI experiment, we combined within subjects
533 longitudinal and between-groups designs. Subsequently, to further test if SPL engagement is
534 behaviorally relevant for performing the same lexical task and if there are hemispheric
535 differences between hearing late learners and deaf signers we conducted a second
536 experiment using TMS.
537
538 ***Sign language processing by hearing learners before the course***
539 During pre-exposure hearing participants had no access to the linguistic meaning of the signs.
540 Thus, they likely performed the task by focusing on the sensory properties of observed
541 meaningless gestures, which was reflected in bilateral activation in the occipitotemporal
542 network (MTG, LOC) involved in visual and motor processing. Additionally, involvement of
543 frontal areas (IFG/PreCG) and parietal regions (postcentral gyrus/SMG extending to the SPL in
544 the right hemisphere) was found, and these areas have been identified as hubs within the
545 mirror neuron system (Buccino et al., 2008; Cattaneo & Rizzolatti, 2009; Rizzolatti & Sinigaglia,
546 2010) – a unified network engaged in processing a broad spectrum of human actions. Notably,
547 participants were aware of the linguistic context of the task and even though they did not
548 know the meaning of signs, they might have tried to extract its linguistic aspects (a similar
549 effect was also discussed by Emmorey et al. (2010) and Liu et al. (2017)).
550
551 This pattern of neural activity is in line with previous results in non-signers performing a task
552 with signs that are meaningless to them (Corina et al., 2007; Emmorey et al., 2010;
553 MacSweeney et al., 2004; 2006; Newman et al., 2015; Williams et al., 2016). With respect to
554 SPL, the activation in the right hemisphere was in line with the findings of Corina et al., (2007),
555 showing common parietal involvement for observation of three types of human action: self-
556 oriented grooming gestures, object-oriented actions, and sign language. In other studies
557 activation of SPL in non-signers observing sign language stimuli was found either in the left
558 hemisphere (MacSweeney et al., 2006; Williams et al., 2016) or in both hemispheres
559 (Emmorey et al., 2010; MacSweeney et al., 2004). Our data suggest the right SPL is dominant
560 during processing of human action that does not contain any linguistic meaning.
561
562 ***Sign language processing by hearing learners after the course and deaf signers***

In line with prior studies of native signers (e.g. Emmorey et al., 2003; 2014; MacSweeney et al., 2006, 2008a; Sakai et al., 2005) and hearing late learners (Johnson et al., 2018; Williams et al., 2016), the classical language region, IFG, located in the left hemisphere responded during the sign language lexical decision task both in HL after the course and deaf signers. In the context of linguistic processes, IFG has been described as a language core mediating language production and comprehension regardless of modality (Binder et al., 2009; Corina & Knapp, 2006; Emmorey et al., 2014; Friederici, 2012; Hickok & Poeppel, 2007; Johnson et al., 2018; MacSweeney et al., 2002, 2008a; Sakai et al., 2005; Williams et al., 2016) and a key node subserving unification, integration and memory retrieval at various linguistic levels (Hagoort, 2013). Additionally, active observation and understanding of action and movement engaged left PreCG, in line with other studies (Emmorey et al., 2014; Schippers & Keysers, 2011).

In addition, HL after the course and deaf signers recruited temporal areas (MTG and ITG) together with occipital regions (LOC), likely reflecting motion-related perception of the body (Emmorey et al., 2014; Liu et al., 2017; MacSweeney et al., 2008a; Williams et al., 2016). Both groups additionally engaged SMG, which has been previously attributed to phonological analysis and working memory demands of sign language (MacSweeney et al., 2008b; Rönnberg et al., 2004). Finally, the activation of bilateral SPL was observed in HL after the course, but deaf individuals showed no involvement of SPL for the lexical decision task.

Further, to investigate with greater precision which regions were prone to activation changes with sign language acquisition in HL, we performed a longitudinal analysis including all TPs. We found that the most pronounced alterations in activity occured predominantly in the left hemisphere – IFG, LOC and SPL. This result suggests that left, but not right SPL, forms a sign language comprehension network over the course of learning. However, no significant changes in SPL activation were observed in previous longitudinal study of Williams and colleagues (2016), which might be due to the linguistically less complex task that they used (i.e., a low level form-based decision).

Several theoretical frameworks and mechanisms for learning-driven brain reorganization have been proposed. For example Wenger et al. (2017) suggested that during learning, neuroplasticity follows a sequence of expansion, selection, and renormalization. In this

context neural alterations would be observed as an initial increase in activation (e.g. through the generation of new dendritic spines or synaptogenesis), which is then followed by partial or complete return to baseline level after an optimal neural circuit has been selected. Although the expansion-renormalization model (Wenger et al., 2017) refers to structural plasticity, it is in line with the neural efficiency theory (Haier et al., 1992), which postulates that better performance on a cognitive task requires fewer neural resources and thus reflects in lower brain activity. However, we found no statistically significant alterations of brain activity after the first three months of PJM learning, despite continued improvements in performance. This result is likely due to the fact that the PJM learners did not reach a level of proficiency that would allow for neural optimization to take place.

Differences in sign language processing between groups

During lexical processing deaf signers, but not HL, engaged STG to a larger extent. This result is in line with previous studies reporting cross-modal plasticity of the auditory cortex in congenitally deaf individuals (e.g. Campbell & MacSweeney, 2004; Cardin et al., 2013; MacSweeney et al., 2008a).

HL before the course had greater activation than deaf signers in the left MFG, a part of the prefrontal system frequently related to a wide range of cognitive functions, i.e. attention: control, selection, orientation etc. (Kane & Engle, 2002; Thompson & Duncan, 2009). It has also been suggested to be a part of the Ventral Attention Network (see Corbetta et al., 2008 for review) and mirror neuron system (Filimon et al., 2007). Thus, this result might suggest enhanced attention and reliance on the sensory aspects of stimuli when sign-naïve participants perform the task.

Lastly, we explored the unique pattern of activation for the same group of hearing participants after they had acquired skills essential for processing the sign stimuli linguistically, in comparison to deaf individuals (HL after the course > deaf signers). We predicted enhanced neural activity in HL, related to greater effort and a lower level of automatization in the lexical processing, compared to fluent deaf signers. Indeed, while the behavioral data did not reveal any group differences, HL exhibited greater involvement in the occipito-parietal visuospatial network – bilateral LOC and left SPL. Greater neural demands in late than early signers (both deaf and hearing) were observed by Twomey and colleagues (2020) in the left occipital

624 segment of intraparietal sulcus, in close proximity to the currently observed cluster in SPL.

625 Similarly in a previous study of Mayberry et al. (2011) on early and late deaf signers, a positive

626 relationship between the age of onset of sign language acquisition and the level of activation

627 in the occipital cortex was found. With the support of previous behavioral data (e.g., Mayberry

628 & Fisher, 1989; Morford et al., 2008), both the Twomey et al. (2020) and the Mayberry et al.

629 (2011) studies suggest shallower language processing and the hypersensitivity to the

630 perceptual properties of signs in late learners. Our results suggest that these greater demands

631 occur not only in the occipital cortex, but also extend to left SPL.

632 ***Differences between the right and left SPL revealed with TMS***

633 Lastly, using TMS we tested if SPL is relevant for sign language comprehension in both deaf

634 signers and hearing late learners and if hemispheric differences are present. Stimulation of

635 both right and left SPL decreased performance compared to the control site (occipital pole).

636 Specifically, TMS stimulation of the right SPL resulted in a decrease in accuracy for both late

637 learners and deaf signers. This finding is in line with insights provided by previous non-

638 linguistic studies, suggesting right-hemisphere dominance in the parietal cortex for

639 visuospatial attention (Cai et al., 2013; Corbalis et al., 2014). In addition, Wu et al. (2016)

640 demonstrated that TMS applied to the right, but not left SPL, resulted in an increase in reaction

641 time for a visuospatial attention task, confirming that the right SPL controls functions

642 supporting visuospatial attention. Here, using a visuospatial linguistic (lexical) task, we suggest

643 the right SPL is also involved in visuospatial attention processes in both skilled and beginning

644 users of sign language. This notion is also supported by the results of Experiment 1, showing

645 no functional changes in the right SPL over the course of sign language learning in the hearing

646 participants.

647

648 Secondly, when TMS pulses were applied to the left SPL, the level of accuracy declined only in

649 the group of HL after the course, as shown by the differential pattern of simple effects.

650 Together with our fMRI result showing an increase in activation when the HL started to

651 comprehend signs, our TMS result suggests that left SPL is linguistically relevant in visuospatial

652 linguistic processing in novice signers. Given the previously reported role of SPL in hand

653 movement processing, we suggest that the left SPL might be more specifically involved in

654 decoding visuospatial aspects of the sign language phonology, such as locations on the face or

body, hand configuration and orientation, and movement trajectories. According to behavioral studies, sign language processing in non-native users is characterised by phonological errors (i.e. Mayberry, 1994; Mayberry & Frisher, 1989; Morford et al., 2008). Mayberry & Fisher (1989) have argued that late learners experience a "phonological bottleneck" that causes more effortful and less automatic access to the lexical meaning of the signs.

Limitations

Several limitations of the current experiment should be noted. First, even though participants performed phonological exercises during the PJM course (e.g., exercises requiring production of signs based on given handshapes), they were never explicitly taught about the phonology of sign language. Although discriminating signs from pseudosigns (created by changing at least one phonological parameter of an existing sign) requires sub-lexical, implicit phonological encoding, the Lexical Decision Task explicitly entails lexical, rather than phonological processing. Therefore our conclusion that the left SPL in hearing learners reflects phonological decoding, based on reverse inference, should be verified in the future based on tasks specifically focused on phonological processing.

Additionally, our paradigm does not disentangle bottom-up perceptual and top-down linguistic processes in the left SPL. In order to make stronger claims about distinct cognitive functions of both left and right SPL, a control non-linguistic task should be implemented in both fMRI and TMS experiments in the future. We also note the TMS localization of the HL group was based on functional activation during the LDT EXP fMRI task, while in deaf group target regions were defined based on anatomical landmarks. We initially aimed to perform an individually-defined localization procedure also in the deaf participants, however, SPL activity could not be localized in the majority of these participants. This inconsistency might be a potential limitation of the current study. Moreover, both HL and deaf signers are difficult to access groups, we consider our sample size in the TMS experiment as relatively small. Lastly, the lack of significant interaction between group (hearing learners/deaf signers) and condition (TMS/no TMS) in the left SPL precludes us from drawing strong inferences about distinct effects of TMS in hearing and deaf participants. Therefore, further studies are needed to confirm our results about the role of SPL in sign language processing.

Conclusions

Taken together, our fMRI and TMS results suggest that SPL participates in the processing of sign language stimuli, however its function might be distinct depending on the hemisphere. Specifically, we propose that right SPL might be involved in the allocation of attention functions and left SPL in the identification and integration of linguistic forms.

Author contributions

AB, ŁB, JM, MŚ, KJ, KE and AM designed the study; BK and MSz developed the software; PM and PR developed stimuli and recruited participants; AB, ŁB, JM and MSz performed the study; AB, ŁB, JM, KJ and AM analyzed data; AB, ŁB, JM, KJ, MŚ, KE and AM interpreted the data; AB wrote the original draft; AB, ŁB, JM, MSz, BK, PM, PR, MŚ, JK, KE, AM wrote, reviewed and edited the final version.

Competing interests

Authors declare no competing interests.

716 **Data availability statement**

717 Partial datasets generated during the current study are available at: https://osf.io/bgjsq/. The

718 conditions of our ethics approval do not permit sharing of the raw MRI data obtained in this

719 study with any individual outside the author team under any circumstances.

720

721 **References**

722 Abutalebi, J. (2008). Neural aspects of second language representation and language control.

723   *Acta Psychologica*, *128*(3), 466–478. https://doi.org/10.1016/j.actpsy.2008.03.014

724 Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system?

725   A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral*

726   *Cortex*, *19*(12), 2767–2796. https://doi.org/10.1093/cercor/bhp055

727 Braun, A. R., Guillemin, A., Hosey, L., & Varga, M. (2001). The neural organization of discourse:

728   An H215O-PET study of narrative production in English and American sign language.

729   *Brain, 124*(10), 2028–2044. https://doi.org/10.1093/brain/124.10.2028

730 Brennan, C., Cao, F., Pedroarena-leal, N., Mcnorgan, C., & Booth, J. R. (2013). Reading

731   Acquisition Reorganized the Phonological Awareness Network Only in Alphabetic

732   Writing Systems. *Human Brain Mapping*, *34*(12), 1–24.

733   https://doi.org/10.1002/hbm.22147.Reading

734 Buccino, G., Binkofski, F., & Riggio, L. (2004). The mirror neuron system and action recognition.

735   *Brain and Language*, *89*(2), 370–376. https://doi.org/10.1016/S0093-934X(03)00356-0

736 Cai, Q., Van der Haegen, L. & Brysbaert, M. (2013). Complementary hemispheric specialization

737   for language production and visuospatial attention. *Proceedings of the National*

738   *Academy of Sciences, 110*, E322–E330. doi:10.1073/pnas.1212956110

739 Cardin, V., Orfanidou, E., Rönnberg, J., Capek, C. M., Rudner, M., & Woll, B. (2013). Dissociating

740   cognitive and sensory neural plasticity in human superior temporal cortex. *Nature*

741   *Communications*, *12* (4). doi:10.1038/ncomms2463

742 Cattaneo, L., Rizzolatti, G. (2009) The mirror neuron system. *Archives of Neurology, 66* (5),

743   557-560. doi:10.1001/archneurol.2009.41

744   Corballis, M.C. (2014). Left brain, right brain: facts and fantasies. *PLoS Biology, 12*(1),
745   e1001767. doi:10.1371/journal.pbio.1001767

746   Corbetta, M., Patel, G. & Shulman, G. L. (2008). The reorienting system of the human brain:
747   from environment to theory of mind. *Neuron, 58(*3), 306-24. doi:
748   10.1016/j.neuron.2008.04.017.

749   Corina, D. P., & Knapp, H. (2006). Sign language processing and the mirror neuron system.
750   *Cortex*, *42*(4), 529–539. https://doi.org/10.1016/S0010-9452(08)70393-9

751   Corina, D., Chiu, Y. S., Knapp, H., Greenwald, R., San Jose-Robertson, L., & Braun, A. (2007).
752   Neural correlates of human action observation in hearing and deaf subjects. *Brain*
753   *Research*, *1152*(1), 111–129. https://doi.org/10.1016/j.brainres.2007.03.054

754   Creem-Regehr, S. (2009). Sensory-motor and cognitive function of the human posterior
755   parietal cortex involved in manual actions. *Neurobiology of Learning and Memory*, *91*(2),
756   166-71, 166–171. doi:10.1016/j.nlm.2008.10.004

757   Emmorey, K. (2002). Language, cognition and the brain: Insights from sign language
758   research. Mahwah, NJ: Lawrence Erlbaum Associates.
759
760   Emmorey, K., Grabowski, T., McCullough, S., Damasio, H., Ponto, L. L. B., Hichwa, R. D, &
761   Bellugi, U (2003). Neural systems underlying lexical retrieval for sign language.
762   *Neuropsychologia*, *41* (1), 85–95. doi.org/10.1016/S0028-3932(02)00089-1
763
764   Emmorey, K., Mehta, S., & Grabowski, T. G. (2007). The neural correlates of sign versus word
765   production. *Neuroimage, 36* (2007), 202-208.
766   doi.org/10.1016/j.neuroimage.2007.02.040

767   Emmorey, K., Xu, J., Gannon, P., Goldin-Meadow, S., & Braun, A. (2010). CNS activation and
768   regional connectivity during pantomime observation: No engagement of the mirror
769   neuron system for deaf signers. *NeuroImage*, *49*(1), 994–1005.
770   https://doi.org/10.1016/j.neuroimage.2009.08.001

771   Emmorey, K., Xu, J., Braun, A. (2011). Neural responses to meaningless pseudosigns: evidence

772   for signes-based phonetic processing in superior temporal cortex. *Brain and Language,*

773   *117*(1), 34-38 https://doi.org/10.1016/j.bandl.2010.10.003.Neural

774   Emmorey, K., McCullough, S., Mehta, S., & Grabowski, T.J. (2014). How sensory-motor systems

775   impact the neural organization for language: Direct contrasts between spoken and

776   signed language. *Frontiers in Psychology*, *5*(MAY), 1–13.

777   https://doi.org/10.3389/fpsyg.2014.00484

778   Emmorey, K., Mehta, S., McCullough, S., & Grabowski, T.G. (2016). The neural circuits

779   recruited for the production of signs and fingerspelled words. *Brain and Language, 160,*

780   30-41. doi.org/10.1016/j.bandl.2016.07.003

781   Filimon, F., Nelson, J. D, Hagler, D. J., & Sereno, M.I (2007). Human cortical representations

782   for reaching: Mirror neurons for execution, observation, and imagery. *Neuroimage*

783   *37*(4), 1315-1328. doi.org/10.1016/j.neuroimage.2007.06.008

784   Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence

785   comprehension. *Trends in Cognitive Sciences, 16*(5), 262–268.

786   https://doi.org/10.1016/j.tics.2012.04.001

787   Hagoort, P. (2013). MUC (memory, unification, control) and beyond. *Frontiers in Psychology*,

788   *4*, 1–13. https://doi.org/10.3389/fpsyg.2013.00416

789   Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature*

790   *Reviews Neuroscience*, *8*(5), 393–402. https://doi.org/10.1038/nrn2113

791   Jednoróg, K., Bola, Ł., Mostowski, P., Szwed, M., Boguszewski, P. M., Marchewka, A., &

792   Rutkowski, P. (2015). Three-dimensional grammar in the brain: Dissociating the neural

793   correlates of natural sign language and manually coded spoken language.

794   *Neuropsychologia*, *71*(April), 191–200.

795   https://doi.org/10.1016/j.neuropsychologia.2015.03.031

796   Johnson, L., Fitzhugh, M. C., Yi, Y., Mickelsen, S., Baxter, L. C., Howard, P., & Rogalsky, C. (2018).

797   Functional Neuroanatomy of Second Language Sentence Comprehension : An fMRI

798   Study of Late Learners of American Sign Language. *Frontiers in Psychology*

799   *9*(September), 1–20. https://doi.org/10.3389/fpsyg.2018.01626

800   Liu, L., Yan, X., Liu, J., Xia, M., Lu, C., Emmorey, K., Chu, M., Ding, G. (2017). Graph theoretical

801   analysis of functional network for comprehension of sign language. *Brain Research*,

802   *1671*, 55–66. https://doi.org/10.1016/j.brainres.2017.06.031

803   MacSweeney, M., Woll, B., Campbell, R., McGuire, P. K., David, A. S., Williams, S. C. R., Suckling,

804   J., Calvert, G. A., & Brammer, M. J. (2002a). Neural systems underlying British Sign

805   Language and audio-visual English processing in native users. *Brain*, *125*(7), 1583–1593.

806   https://doi.org/10.1093/brain/awf153

807   MacSweeney, M., Woll, B., Campbell, R., Calvert, G. A., McGuire, P. K., David, A. S., Simmons,

808   A., & Brammer, M. J. (2002b). Neural Correlates of British Sign Language

809   Comprehension: Spatial Processing Demands of Topographic Language. *Journal of*

810   *Cognitive Neuroscience, 14*(7), 1064–1075.

811   https://doi.org/10.1162/089892902320474517

812   MacSweeney, M., Campbell, R., Woll, B., Giampietro, V., David, A. S., McGuire, P. K., Calvert,

813   G. A., & Brammer, M. J. (2004). Dissociating linguistic and nonlinguistic gestural

814   communication in the brain. *NeuroImage*, 22(4), 1605–1618.

815   https://doi.org/10.1016/j.neuroimage.2004.03.015

816   MacSweeney, M., Campbell, R., Woll, B., Brammer, M. J., Giampietro, V., David, A. S., Calvert,

817   G. A., & McGuire, P. K. (2006). Lexical and sentential processing in British Sign Language.

818   *Human Brain Mapping*, *27*(1), 63–76. https://doi.org/10.1002/hbm.20167

819   MacSweeney, M., Capek, C. M., Campbell, R., & Woll, B. (2008a). The signing brain: the

820   neurobiology of sign language. *Trends in Cognitive Sciences*, *12*(11), 432–440.

821   https://doi.org/10.1016/j.tics.2008.07.010

822   MacSweeney, M., Waters, D., Brammer, M. J., Woll, B., & Goswami, U. (2008b). Phonological

823   processing in deaf signers and the impact of age of first language acquisition.

824   *NeuroImage*, *40*(3), 1369–1379. https://doi.org/10.1016/j.neuroimage.2007.12.047

825   MacSweeney, M., & Emmorey, K. (2020). The neurobiology of sign language processing. In D.
826   Poeppel, G. Mangun, and M. Gazzaniga (Eds.), *The Cognitive Neurosciences VI,* pp. 851–
827   858, Cambridge, MA: The MIT Press.

828   Mayberry, R.I., & Fischer, S. D. (1989). Looking through phonological shape to lexical meaning:
829   The bottleneck of non-native sign language processing. *Memory & Cognition, 17*(6),
830   740–754. doi: 10.3758/BF03202635

831   Mayberry, R. I. (1994). The importance of childhood to language acquisition: Evidence from
832   American Sign Language. In: Goodman JC, Nusbaum HC, editors. The development of
833   speech perception: The transition from speech sounds to spoken words. Cambridge,
834   MA: *The MIT Press*; pp. 57–90.

835   Mayberry, R.I., Chen, J. K., Witcher P., Klein D. (2011). Age of acquisition effects on the
836   functional organization of language in the adult brain. *Brain and Language 119*(1), 16 –
837   29. doi:10.1016/j.bandl.2011.05.007

838   McCullough, S., Saygin, A. P., Korpics, F., & Emmorey, K. (2012). Motion-sensitive cortex and
839   motion semantics in American Sign Language. *NeuroImage, 63*(1), 111–118.
840   https://doi.org/10.1016/j.neuroimage.2012.06.029

841   Morford, J., Grieve-Smith, A. B., MacFarlane, J., Stanley, J., & Waters, G. (2008). Effects of
842   language experience on the perception of American Sign Language. *Cognition*, *109*(1),
843   41–53. doi: 10.1016/j.cognition.2008.07.016

844   Newman, A. J., Supalla, T., Fernandez, N., Newport, E. L., & Bavelier, D. (2015). Neural systems
845   supporting linguistic structure, linguistic experience, and symbolic communication in sign
846   language and gesture. *Proceedings of the National Academy of Sciences, 112*(37), 11684–
847   11689. https://doi.org/10.1073/pnas.1510527112

848   Poeppel, D., Emmorey, K., Hickok, G., & Pylkkanen, L. (2012). Towards a new neurobiology of
849   language. *Journal of Neuroscience*, *32*(41), 14125–14131.
850   https://doi.org/10.1523/JNEUROSCI.3244-12.2012

851 Rizzolatti, G., Sinigaglia, C., (2008). Mirrors in the Brain. How our minds share actions and
852   emotions. *Oxford University Press*.

853 Rönnberg, J., Rudner, M., & Ingvar, M. (2004). Neural correlates of working memory for sign
854   language. *Cognitive Brain Research*, *20*(2), 165–182.
855   https://doi.org/10.1016/j.cogbrainres.2004.03.002

856 Sakai, K. L., Tatsuno, Y., Suzuki, K., Kimura, H., & Ichida, Y. (2005). Sign and speech: Amodal
857   commonality in left hemisphere dominance for comprehension of sentences. *Brain*,
858   *128*(6), 1407–1417. https://doi.org/10.1093/brain/awh465

859 Sadato, N., Okada, T., Honda, M., Matsuki, K-I., Yoshida, M., Kashikura, K-I., Takei, W., Sato, T.,
860   Kochiyama, T., & Yonekura, Y. (2005). Cross-modal integration and plastic changes
861   revealed by lip movement, random-dot motion and sign languages in the hearing deaf.
862   *Cerebral Cortex*, 15, 1113-1122. https://doi.org/10.1093/cercor/bhh210

863 Schippers, M. B., & Keysers, C. (2011). Mapping the flow of information within the putative
864   mirror neuron system during gesture observation. *NeuroImage*, *57*(1), 37–44.
865   https://doi.org/10.1016/j.neuroimage.2011.02.018

866 Stowe, L. A, & Sabourin, L. (2005). Imaging the processing of a second language: Effects of
867   maturation and proficiency on the neural processes involved. *International Review of*
868   *Applied Linguistics in Language Teaching*, *43*, 329–353. doi: 10.1515/iral.2005.43.4.329
869
870 Twomey, T., Price, C. J., Waters, D., & MacSweeney, M. (2020). The impact of early language
871   exposure on the neural system supporting language in deaf and hearing adults.
872   *Neuroimage, 201*(1), 116411. doi:10.1016/j.neuroimage.2019.116411
873
874 van Heuven, W. J. B., & Dijkstra, T. (2010). Language comprehension in the bilingual brain:
875   fMRI and ERP support for psycholinguistic models. *Brain Research Reviews*, 64(1), 104–
876   122. doi: 10.1016/j.brainresrev.2010.03.002

877 Williams, J. T., Darcy, I., & Newman, S. D. (2016). Modality-specific processing precedes
878   amodal linguistic processing during L2 sign language acquisition: A longitudinal study.
879   1*Cortex*, *75*, 56–67. https://doi.org/10.1016/j.cortex.2015.11.015

880   Wu, Y., Wang, J., Zhang, Y., Zheng, D., & Zhang, J. (2016). The Neuroanatomical Basis for

881   Posterior Superior Parietal Lobule Control Lateralization of Visuospatial Attention.

882   *Frontiers in Neuroanatomy*, *10*:32. doi: 10.3389/fnana.2016.00032

883

884

885