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Neural correlates of semantic and syntactic processing in German Sign Language

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ABSTRACT

The study of deaf and hearing native users of signed languages can offer unique insights into how biological constraints and environmental input interact to shape the neural bases of language processing. Here, we use functional magnetic resonance imaging (fMRI) to address two questions: (1) Do semantic and syntactic processing in a signed language rely on anatomically and functionally distinct neural substrates as it has been shown for spoken languages? and (2) Does hearing status affect the neural correlates of these two types of linguistic processing? Deaf and hearing native signers performed a sentence judgement task on German Sign Language (Deutsche Gebärdensprache: DGS) sentences which were correct or contained either syntactic or semantic violations. We hypothesized that processing of semantic and syntactic violations in DGS relies on distinct neural substrates as it has been shown for spoken languages. Moreover, we hypothesized that effects of hearing status are observed within auditory regions, as deaf native signers have been shown to activate auditory areas to a greater extent than hearing native signers when processing a signed language. Semantic processing activated low-level visual areas and the left inferior frontal gyrus (IFG), suggesting both modality-dependent and independent processing mechanisms. Syntactic processing elicited increased activation in the right supramarginal gyrus (SMG). Moreover, psychophysiological interaction (PPI) analyses revealed a cluster in left middle occipital regions showing increased functional coupling with the right SMG during syntactic relative to semantic processing, possibly indicating spatial processing mechanisms that are specific to signed syntax. Effects of hearing status were observed in the right superior temporal cortex (STC): deaf but not hearing native signers showed greater activation for semantic violations than for syntactic violations in this region. Taken together, the present findings suggest that the neural correlates of language processing are partly determined by biological constraints, but that they may additionally be influenced by the unique processing demands of the language modality and different sensory experiences.

1. Introduction

During development, the structural and functional organization of the brain is typically shaped by interactions between genetic predispositions and environmental input. The study of deaf and hearing native users of signed languages (SL) offers valuable insights into how those two factors interact. Since SL have radically different surface form characteristics than spoken languages (SpL), the comparison of SpL and SL comprehension allows us to identify linguistic processing mechanisms that are universal to human language and those that are tied to certain sensorimotor systems. In addition, by comparing deaf and hearing native signers it is possible to delineate the effects of different sensory experiences and those of acquiring a language that operates in a visuo-manual rather than an aural-oral modality.

1.1. Semantic and syntactic processing in SL

While the purpose of language processing is the same across modalities, i.e. the comprehension and production of meaning, the neural mechanisms through which it can be achieved might be influenced by the modality of the language. Neuroimaging and lesion studies have suggested that the systems involved in language comprehension are remarkably similar for SL and SpL processing and thus largely independent of the sensory modality (Atkinson et al., 2005; Hickok et al., 1996; Hickok et al., 2002; MacSweeney et al., 2002; see MacSweeney et al., 2008 for a review; Neville et al., 1998; Petitto et al., 2000; Poizner et al., 1987; Sakai et al., 2005). However, some evidence has suggested that certain aspects of signed grammar, such as verb agreement, engage spatial processing mechanisms that are specific to the signed modality (Capek et al., 2009).

One prominent feature of SL is the use of space to express grammatical relations: To this end, SL use spatial loci, direction of movement and/or hand orientations. One example of the use of space in SL is verb agreement. In SL verb agreement is expressed through a movement from the location of the subject to the location of the object. For example, in the DGS translation of the sentence “The girl visits the boy” (see Fig. 1),

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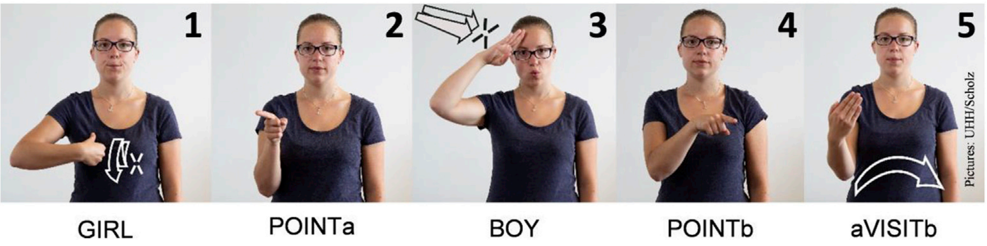

Fig. 1. Illustration of verb agreement in a DGS sentence. Shown is the DGS translation of the sentence “The girl visits the boy” and the DGS glosses. Picture 1: lexical sign for GIRL. Picture 2: referential location for GIRL established by indexing to the right. Picture 3: lexical sign for BOY. Picture 4: referential location for BOY established by indexing to the left. Picture 5: the verb VISITS moves from the location assigned to the GIRL towards the location assigned to the BOY.

the verb (“visits”) moves from the location assigned to the subject (“girl”) towards the location assigned to the object (“boy”).

Despite extensive research investigating the neural systems mediating SL, relatively little is known about the neural systems supporting different aspects of SL processing such as syntax and semantics. One common approach to isolate semantic and syntactic processing is to compare the processing of sentences containing semantic or syntactic violations with the processing of the corresponding correct sentences. This approach has been employed extensively by studies investigating syntactic and semantic processing in SpL using event-related potentials (ERPs), in which different ERP components have been observed for syntactic and semantic violations (Friederici et al., 1993; Kutas and Hillyard, 1984; Neville et al., 1991; Osterhout and Mobley, 1995). fMRI studies which used this paradigm have indicated that semantic and syntactic processing recruit distinct subregions of the left inferior frontal gyrus (IFG) and the left superior temporal cortex (STC) (Dapretto and Bookheimer, 1999; see Hagoort and Indefrey, 2014 for a review; Ni et al., 2000).

So far, only few EEG studies have used this approach to study semantic and syntactic aspects of SL. While the effects of semantic processing are very similar across the two language modalities (Capek et al., 2009; Gutierrez et al., 2012; Hänel-Faulhaber et al., 2014), the situation seems to be somewhat different for syntactic processing. Syntactic effects are similar in SpL and SL with respect to the temporal aspects of processing (Capek et al., 2009; Hänel-Faulhaber et al., 2014). However, differences between SpL and SL have been observed in the topographical distribution of the left anterior negativity. In particular, Capek et al. (2009) used two types of syntactic violations: a reversed verb agreement violation where the verb moved towards the subject instead of the object and an unspecified verb agreement violation where the verb moved towards a location in space that had not been defined previously as the subject or object. Both types of violation elicited an anterior negativity followed by a widely distributed P600. However, the distribution of the anterior negativity varied as a function of the type of syntactic violation. Reversed verb-agreement violations elicited an early anterior negativity that was largest over the left hemisphere, which was similar to what has been reported in studies of written and spoken language processing. In contrast, unspecified verb agreement violations elicited an anterior negativity that was larger over the right hemisphere. Capek et al. (2009) thus suggested that these two types of verb agreement violations place different demands on the systems involved in processing spatial aspects of signed syntax. As the topography of EEG data cannot reveal the exact location of underlying neural generators, these results raise the question of what the underlying neural correlates of these processing differences between signed and spoken syntax are, specifically, whether they result from a differential recruitment of areas known to be involved in spatial processing.

1.2. *Effects of hearing status on the neural bases of language processing*

Neuroimaging studies have suggested that during SL processing deaf signers recruit superior temporal cortices to a greater extent than hearing signers (MacSweeney et al., 2002; Twomey et al., 2017). In hearing people the STC is the site of auditory association cortex and plays a crucial role in speech processing (DeWitt and Rauschecker, 2012). Within the left STC and mid to anterior parts of the right STC the recruitment in deaf individuals during SL processing seems to reflect linguistic rather than basic visual processing (Cardin et al., 2013; Twomey et al., 2017). In a recent study by Twomey et al. (2017) deaf but not hearing signers recruited the left STC during a phonological but not during a semantic SL task, indicating that hearing status can have differential effects on specific aspects of linguistic processing. Other studies have found that the left and the right STC of deaf signers were activated during the processing of lexicosemantic aspects of SL (Emmorey et al., 2013; Leonard et al., 2012), just as it has been proposed for SpL (DeWitt and Rauschecker, 2012). However, these studies did not compare deaf and hearing signers, thus it is difficult to assess whether semantic processing for SL within these regions is independent of the hearing status of the subjects or not.

1.3. *The present study*

The goal of the present study was twofold: (i) to identify the neural correlates of syntactic and semantic processing in SL, and (ii) to investigate the effects of hearing status on the processing of these two types of linguistic information in SL. To this end, we presented DGS sentences that were either well-formed or contained syntactic or semantic violations to two groups of native signers who were either deaf or hearing. Participants performed a sentence judgement task while undergoing fMRI. Based on the above-mentioned ERP studies we hypothesized that semantic processing is independent of the modality, while syntactic processing in DGS involves modality-dependent processing mechanisms that are related to the spatial aspects of signed grammar. We thus expected semantic processing in DGS to recruit the left inferior frontal cortex and the left temporal cortex as has been found for SpL, and syntactic processing to recruit brain areas that are involved in spatial processing, such as the parietal cortex. Moreover, given that deaf native signers have been shown to recruit auditory areas to a greater extent than hearing native signers when processing SL (MacSweeney et al., 2002), we hypothesized that effects of hearing status would be observed within auditory regions.

2. Materials and methods

2.1. *Participants*

Eight deaf native signers (age (M) = 31.71 years±2.03 s.e.m.; 4 females) and eight hearing native signers (age (M) = 30.25 years ±1.72 s.e.m.; 5 females) participated in the experiment which was part of a larger study investigating modality differences in language processing. During the same session, both deaf and hearing participants completed the DGS experiment reported here and an fMRI experiment where they viewed similar sentence material in written German language. Hearing signers additionally completed the same task with audio-visual language stimuli. All of the participants were born to deaf parents and acquired DGS as their first language from birth. All of the participants were right-handed (Oldfield Handedness Inventory score: deaf signers: 90 (Median, range = 70–100), hearing signers: 90 (Median, range = 60–100)). All deaf participants indicated that they had always communicated with their parents in DGS, whereas hearing participants indicated that they had communicated with their parents in a mixture of DGS, sign supported speech ("lautsprachbegleitende Gebärden", LBG), and SpL (German) during childhood. All deaf participants reported that they use DGS as their primary means of communication on a daily basis, whereas hearing participants reported that they use DGS at least once a week. SL proficiency of the participants was assessed with the "Gebärdensprach-Sinnverständnis Test" (GSV) of the "Aachener Testverfahren zur Berufseignung von Gehörlosen" (ATGB). The GSV is a narrative comprehension task and involves watching narratives in DGS and answering multiple-choice questions. The GSV-scores in deaf native signers (Median = 90% correct, range = 85–100%) did not differ significantly from hearing native signers (Median = 85% correct, range = 45–95%), W = 43, $p = .261$. In addition to the GSV, we asked the participants to self-rate their DGS skills. All of the deaf signers indicated their level of comprehension and production of DGS to be 1 on a scale of 1–4 (1 = excellent, 4 = not very good at all), whereas the hearing signers indicated their level of comprehension to be 2 (Median, range = 1–3) and their level of production to be 2.5 (Median, range = 1–3). All of the deaf native signers were congenitally deaf and reported severe hearing loss (>85 dB in the better ear). All participants had normal or corrected to normal vision and none reported any history of psychiatric or neurological disorders.

All participants gave written informed consent and received a monetary compensation for their participation. The experiment was approved by the ethics committee of the German Society for Psychology (DGPS; reference number: BRBHF07022006).

2.2. Experimental procedure

The stimuli were from Hänel-Faulhaber et al. (2014) and consisted of videos of DGS sentences. In total, the experimental protocol comprised 144 sentences, which lasted between 5.4 and 13.8 s. Seventy-two of the sentences were correct and the remaining 72 contained a violation. Half of the correct sentences served as a base for constructing sentences that contained either a semantic or a syntactic violation. The semantic violations consisted of a selectional restriction violation where the object-verb relation was semantically not plausible (see Table 1 for examples). Since DGS is a subject-object-verb (SOV) language, the sentences containing semantic violations became implausible at the verb. Sentences containing a syntactic violation included an incorrect inflection of the verb, that is, an incorrect direction of movement from neutral space to the first person. Thus, the violation always appeared at the verb, irrespective of the type of violation. In addition, 36 filler sentences varying in verb types (i.e. classifier verbs) or sentence constructions (i.e. causal clauses) were included to reduce the predictability of the sentence structure. Thus, the total stimulus set comprised 144 sentences, of which 72 were correct sentences, 36 were sentences containing a semantic violation and another 36 were sentences containing a syntactic violation.

Table 1
Example sentences. Violations are indicated with a *.

condition	example sentence
correct	STUDENT PERSONa POINTa HISa CLASS MATE PERSONb INFORMb LESSON CANCELLED "The student informs his classmate that the lesson is cancelled."
semantic violation	STUDENT PERSONa POINTa HISa *BOOK POINTb INFORMb LESSON CANCELLED "The student informs his *book that the lesson is cancelled."
syntactic verb-agreement violation	STUDENT PERSONa POINTa HISa CLASS MATE PERSONb *INFORM1 LESSON CANCELLED "The student *inform his classmate that the lesson is cancelled."

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Before entering the scanner, the tasks were explained to the participants in their preferred language (in German or in DGS by a fluent signer). Following this, the participants completed a practice run to ensure that they had understood and were comfortable with the task. Each participant completed three scanning runs. The first two runs consisted of 50 sentences and the third run consisted of 44 sentences. The different trial types were presented in a random order. At the end of each sentence, a grey screen appeared for 2 s, followed by a happy and a sad smiley. When the smileys appeared on the screen, participants had to decide whether the sentence was correct or not via a button press with either the left or right index finger. The hand used to indicate the response options was randomised across participants. No performance feedback was given and the next trial began after an inter-trial interval that lasted on average 4.2 s. The stimuli were projected onto a screen and viewed via mirrors attached to the head coil. Overall, each run lasted approximately 14 min. Participants had the opportunity to take short breaks in between runs. On average, breaks lasted approximately 2 min.

2.3. Data acquisition

Functional images were acquired sequentially from inferior to superior with a 3-T MRI system (Siemens Magnetom Trio, Erlangen, Germany; circularly polarized eight-channel head coil; repetition time (TR) = 2300 ms, TE = 30 ms, FOV 216 × 216 mm, voxel size = 3 mm^3, 40 slices, flip angle = 80°, aligned to the AC-PC line) using echo-planar imaging (EPI). Anatomical images were collected using T1-weighted inversion recovery prepared EPI (IR-EPI) sequences (TR = 2300 ms, TE = 2.98 ms, FOV: 192 × 192 mm, voxel size = 1 mm^3, 240 slices, flip angle = 9°). Task presentation and recording of behavioural responses were conducted with Presentation software (www.neurobs.com).

2.4. fMRI preprocessing and analysis

The fMRI data were pre-processed and analysed using SPM8 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK) and MATLAB R2013a (The MathWorks, Inc., Natick, MA, USA). The first five volumes of each run were discarded to allow for signal equilibration. The data pre-processing steps included slice-timing correction, realignment, coregistration, segmentation, spatial normalization to MNI standard space and spatial smoothing (8 mm full width at half maximum (FWHM) Gaussian kernel).

2.4.1. Activation analyses

The fMRI analysis, based on a mixed effects model, was conducted in two serial steps accounting respectively for fixed and random effects. For each subject, changes in brain regional responses were estimated through a general linear model (GLM) with regressors representing each stimulus category (correct sentences, sentences containing a syntactic violation, sentences containing a semantic violation, correct filler sentences), jitter, cue and response periods, and error trials (i.e. trials where the subject did not respond correctly). These regressors consisted of a boxcar function convolved with the canonical hemodynamic response function. Fixation periods between the trials served as a baseline and were modelled implicitly. Movement parameters derived from the realignment of the functional volumes (translations in x, y and z directions and rotations around x, y and z axes) and a constant vector were also included as covariates of no interest. High-pass filtering was implemented in the design matrix using a cut-off period of 128 s to remove slow drifts from the time series. Serial correlations in fMRI signal were estimated using an autoregressive (order 1) plus white noise model and a restricted maximum likelihood (ReML) algorithm.

Four linear contrasts were created for each participant and respectively tested the processing of semantic violations [semantic violations > correct], the processing of syntactic violations [syntactic violations > correct], distinct effects of processing semantic violations [semantic violations > syntactic violations] and syntactic violations [syntactic violations > semantic violations]. The resulting contrast images were spatially smoothed (Gaussian kernel 6 mm FWHM) and entered into a second-level analysis, corresponding to a random effects model, accounting for inter-subject variance.

For each contrast, one-sample t-tests were conducted in each group separately and are reported in supplementary material. In order to identify areas of the brain that are involved in syntactic and semantic processing during SL comprehension irrespective of hearing status, we performed a global conjunction analysis. Two-sample t-tests were then used to compare these effects between groups and to identify areas that are affected by hearing status.

2.4.2. *Functional connectivity analyses*

Psychophysiological interaction (PPI) analyses identify voxels which show an effect in the functional connectivity with the seed region of interest (ROI) in a given psychological context (Gitelman et al., 2003). These analyses were exploratory in nature and were conducted in order to identify brain regions which showed increased functional coupling with the right supramarginal gyrus while processing syntactic violations relative to semantic violations. The seed ROI was selected on the basis of the significantly activated cluster from the contrast [SYN >SEM], located in the right supramarginal gyrus [48 -40 55]. This region has been hypothesized to play a crucial role in the processing of signed syntax (Corina et al., 2012). The group cluster peak was used as a point of reference to identify individual peaks in each subject within a sphere of 5 mm radius. The peak of each subject was used as a centre to create individual volumes of interest (VOI) of 5 mm radius within each participant.

New contrasts were generated at the individual level, using three regressors of interest. The first regressor represented the activity extracted in the seed area. The second regressor represented the condition ([SYN >SEM]). The third regressor represented the interaction of interest between the first (physiological) and the second (psychological) regressor. To build the third regressor, the underlying neuronal activity was first estimated by a parametric empirical Bayes formulation, combined with the psychological factor and subsequently convolved with the hemodynamic response function (Gitelman et al., 2003). Movement parameters were also included in the design matrix as a regressor of no interest. Voxels with a significant context-dependent increase in coupling with the seed region were identified using a T-contrast on the third regressor of interest. The resulting contrast images were spatially smoothed (Gaussian kernel 6 mm FWHM).

Individual contrast images were entered into a second-level random effects analysis in which functional connectivity between the seed region and other regions of the brain was assessed with a global conjunction analysis across the two groups. A significant PPI indicated a change in the regression coefficients between any reported brain area and the seed area, related to the experimental condition ([SYN >SEM]). The voxels identified in this analysis show a pattern of activity correlated with the seed region during the syntactic relative to the semantic condition.

Considering the limited sample size, we backed up the parametric results of the univariate and PPI analyses with additional tests using nonparametric permutation and randomisation techniques via the SnPM13 toolbox (Nichols and Holmes, 2002). These analyses revealed activation patterns that were consistent with the ones detected with the parametric tests (see Supplementary Material Tables 1–4).

All local maxima are reported as MNI coordinates. Relevant anatomical landmarks were identified with the Anatomy Toolbox (Eickhoff et al., 2005; http://www.fz-juelich.de/ime/spm_anatomy_toolbox).

2.4.3. *Statistical inference*

The resulting set of voxel values for each contrast in the univariate and PPI analyses constituted a map of the t-statistic [SPM(T)] that was thresholded at $p < .001$ (uncorrected for multiple comparisons) in combination with a cluster threshold of 10 contiguous voxels. For the univariate analyses, statistical inference was performed at the peak level using a threshold of $p < .05$ after correction for multiple comparisons (Family Wise Error method (FWE)) either over the entire brain volume, or over anatomical regions of interest. Bilateral superior temporal cortices (STC) were included as anatomical regions of interest since we expected to find effects of hearing status within these regions. Correction within bilateral STC was based on masks of the left and right STC (see Fig. 1 in supplementary material) taken from the AAL ROI library (Tzourio-Mazoyer et al., 2002) and created with Marsbar (Brett, Anton, Valabregue and Poline, 2002). Given that PPI analyses were exploratory in nature and considering the lack of power for connectivity analyses (O'Reilly et al., 2012), all coordinates passing the threshold of $p < .001$ (uncorrected for multiple comparisons) in combination with a cluster extent of 10 contiguous voxels are reported, but they are only discussed if they reached a significance threshold of $p < .05$ (FWE corrected) at peak level.

3. Results

3.1. *Behavioural results*

We used the package lme4 (Bates et al., 2015) in the R environment (R Development Core Team, 2008) to perform a mixed effects logistic regression analysis of the behavioural data. The binary target variable was accuracy at each trial (i.e. correct vs. incorrect response). As fixed effects, we entered group (two levels: deaf signers, hearing signers), condition (three levels: semantic violation, syntactic violation, correct) and group*condition interaction into the model. As random effects, we had intercepts for subjects. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. Post-hoc comparisons of significant effects were conducted using approximate z-tests on the estimated marginal means (emm) (Lenth, 2019). The resulting p-values were corrected for multiple comparisons following the procedure proposed by Holm (1979). See Table 2.

There was a main effect of group, $\chi^2(1) = 4.47$, $p = .034$. Post-hoc comparisons revealed that hearing signers (emm = 2.74, CI [1.99; 3.49]) responded less accurately than deaf signers (emm = 3.96, CI [3.06; 4.85]), $\beta = -1.220$, SE = 0.591, z-ratio = -2.064, $p = .039$. There was a main effect of condition, $\chi^2(2) = 26.85$, $p < .001$. Post-hoc comparisons revealed that participants responded more accurately in the correct condition (emm = 3.54, CI [2.85; 4.22]) than in the syntactic condition (emm = 2.64, CI [2.03; 3.25]), $\beta = .895$, SE = 0.259, z = 3.458, $p = .001$. Participants also responded more accurately in the semantic condition (emm = 3.86, CI [3.13; 4.59]) than in the syntactic condition (emm = 2.64, CI [2.03; 3.25]), $\beta = 1.216$, SE = 0.289, z-ratio = 4.210, $p < .001$. There was no interaction between group and condition, $\chi^2(2) = 0.23$, $p = .893$.

Table 2
Mean performance on the sentence judgement task. Standard error of the mean in parentheses.

Condition	Accuracy		**Averaged over condition**
	Deaf Signers	Hearing Signers	
Correct	96.88 (6.71)	94.10 (5.44)	95.49 (6.08)
Semantic violation	97.92 (3.24)	95.12 (4.13)	96.52 (3.87)
Syntactic violation	93.75 (12.40)	85.76 (12.37)	89.76 (12.66)
Averaged over group	96.18 (8.18)	91.66 (8.90)	

3.2. fMRI results

3.2.1. Semantic processing

The group conjunction contrast [SEM > CORR] identified areas of the brain involved in processing semantic violations. This contrast revealed activation in the left calcarine sulcus and the right hippocampus (see Fig. 2, Table 3). Brain areas more responsive during semantic than syntactic processing were identified using the contrast [SEM > SYN]. This contrast revealed activation in pars orbitalis and pars triangularis of the left IFG (see Fig. 3, Table 3).

3.2.2. Syntactic processing

The contrast [SYN > CORR] identified brain areas involved in processing syntactic violations. This contrast revealed activation in the right supramarginal gyrus (SMG, area PFm; see Fig. 4, Table 4). In a next step, we identified areas that are more activated in syntactic compared to semantic processing, using the contrast [SYN >SEM]. This contrast revealed activation in the right SMG (area PFm and PFt) extending into the inferior parietal sulcus and the superior parietal lobule (see Fig. 5, Table 4).

An examination of these effects separately in each group revealed an activation pattern that was consistent with the effects reported in the conjunction analyses, ascertaining that the reported effects were not driven by one group or the other (see Supplementary Material Figs. 2–5).

3.2.3. PPI results

PPI analyses revealed clusters showing increased functional coupling with the right SMG during syntactic relative to semantic processing in the left middle occipital gyrus that included parts of area hOc5 (Malikovic et al., 2007), the pars triangularis of the right IFG, the left middle temporal gyrus, and the precentral gyrus bilaterally (see Fig. 6 and Table 5). Examination of these effects separately in each group revealed a response pattern that was consistent with the effects reported in the conjunction analyses, ascertaining that the reported effects were not driven by one group or another (see Supplementary Material Fig. 6).

3.2.4. Effects of hearing status

In order to identify regions that show effects of hearing status on SL processing, we compared the effects between the two groups using two-sample t-tests [Deaf > Hearing] × [SEM > SYN]. This analysis revealed a cluster in the middle portion of the right STC (mSTC; see Fig. 7, Table 6). Deaf signers showed greater activation for semantic violations than for syntactic violations (*Z-score*: 4.32, $p = .003$ (corrected for FWE over the anatomical region of interest)), whereas hearing signers did not show a significant effect of condition in this region.

4. Discussion

The goal of this study was to investigate the neural correlates of semantic and syntactic processing in DGS and to assess whether hearing status influences these neural correlates. To this end, we compared cortical responses of deaf and hearing native signers during the processing of DGS sentences containing semantic and syntactic violations. Semantic violations compared to correct sentences elicited increased activation in low-level visual areas in both groups of native signers, suggesting modality-specific processing mechanisms. Semantic compared to syntactic violations elicited increased activation in the left IFG. This concurs with findings from spoken and written language studies (see Hagoort and Indefrey, 2014 for a review), suggesting modality-independent processing mechanisms for linguistic core functions. Syntactic violations compared to correct sentences involved increased activation in the right supramarginal gyrus, possibly indicating spatial processing mechanisms that are specific to signed syntax (Bavelier et al., 1998; Neville et al., 1998; Newman et al., 2002). This activation was violation specific, as syntactic violations compared to semantic violations elicited increased activation in this area as well. Effects of hearing status were observed in the right STC: deaf but not hearing signers showed greater activation for semantic violations than for syntactic violations.

Table 3

Coordinates and statistics for the effects of semantic violations. Coordinates in this table are reported if significant ($p < .05$) after correction over the whole brain. *k* represents the number of voxels when displayed at $p_{(\text{uncorrected})} < .001$.

Area	k	p (FWE-corr)	Z-score	x	y	z
SEM vs CORR						
left calcarine sulcus	447	<.001	5.81	−3	−85	10
right hippocampus	37	.024	4.82	36	−28	−5
SEM vs SYN						
left inferior frontal gyrus (pars triangularis)	70	.003	5.18	−45	32	16
left inferior frontal gyrus (pars orbitalis)	24	.031	4.66	−42	35	−17

4.1. Semantic processing

Both deaf and hearing signers showed greater activation in the left calcarine sulcus when processing semantic violations compared to correct sentences (see Fig. 2). It could be argued that these effects are due to low-level visual differences between the two conditions. However, we consider this account of our results as unlikely, since correct sentences were matched in their low-level visual features, so that any differences between the two conditions cannot be attributed to differences in low-level visual features (Neville et al., 1998). Previous studies have suggested that such effects could possibly reflect early sensory prediction errors as it has been shown that humans use contextual cues during

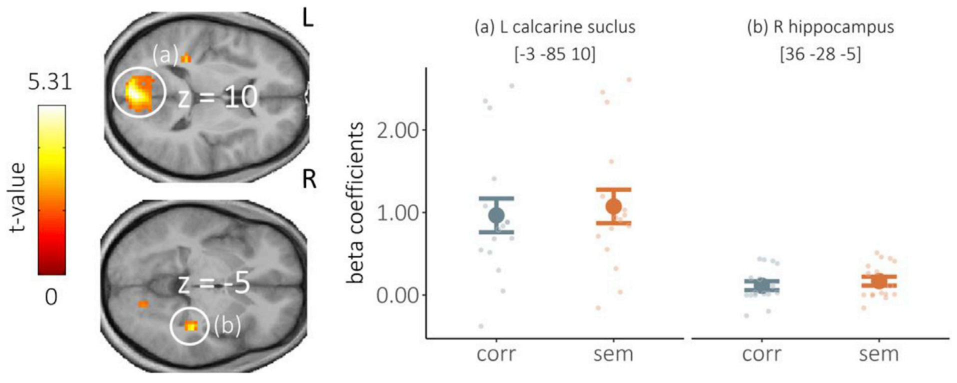

Fig. 2. Effects of semantic violations in the visual cortex (a, top panel) and the right hippocampus (b, bottom panel) of signers. The effect of semantic violations was assessed with a conjunction of T-contrasts [SEM > CORR] across two groups of signers (deaf signers and hearing signers). For illustration, mean parameter estimates (arbitrary units ± SEM) at significant peaks are plotted separately for each condition. Results are overlaid on transverse slices of the mean structural image of all of the participants. Images are displayed at a threshold of $p < .001$ (uncorrected) with a spatial extent threshold of 10 voxels. Colour bars represent t-values. Coordinates are in Montreal National Institute (MNI) space. L = left, R = right. See Table 3 for a list of regions depicted in this figure. See also Supplementary Fig. 2.

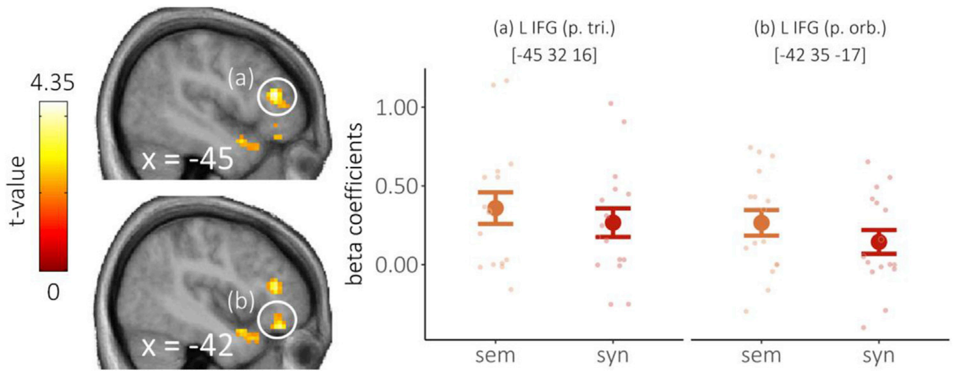

Fig. 3. Effects of semantic violations in the left inferior frontal gyrus of signers. The effect of semantic violations was assessed with a conjunction of T-contrasts [SEM > SYN] across two groups of signers (deaf signers and hearing signers). Top panel: Effect of semantic violations in the in the pars triangularis (a). Bottom panel: Effect of semantic violations in the pars orbitalis (b). For illustration, mean parameter estimates (arbitrary units ± SEM) at significant peaks are plotted separately for each condition. Results are overlaid on sagittal slices of the mean structural image of all of the participants. Images are displayed at a threshold of $p < .001$ (uncorrected) with a spatial extent threshold of 10 voxels. Colour bars represent t-values. Coordinates are in Montreal National Institute (MNI) space. L = left, IFG = inferior frontal gyrus. See Table 3 for a list of regions depicted in this figure. See also Supplementary Fig. 3.

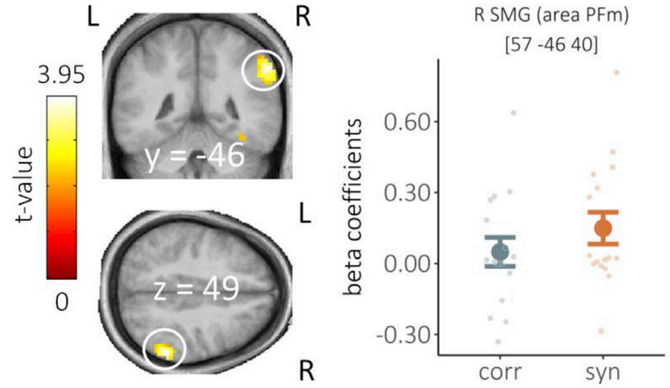

Fig. 4. Effects of syntactic violations in the inferior parietal cortex of signers. The effect of syntactic violations was assessed with a conjunction of T-contrasts [SYN > CORR] across two groups of signers (deaf signers and hearing signers). For illustration, mean parameter estimates (arbitrary units ± SEM) at significant peaks are plotted separately for each condition. Results are overlaid on a coronal (upper panel) and a transverse slice (lower panel) of the mean structural image of all of the participants. Images are displayed at a threshold of $p < .001$ (uncorrected) with a spatial extent threshold of 10 voxels. Colour bars represent t-values. Coordinates are in Montreal National Institute (MNI) space. L = left, R = right, SMG = supramarginal gyrus. See Table 4 for a list of regions depicted in this figure. See also Supplementary Fig. 4.

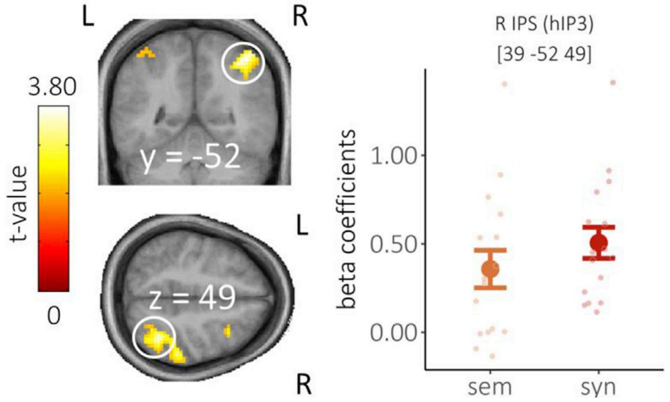

Fig. 5. Effects of syntactic violations in the inferior parietal cortex of signers. The effect of syntactic violations was assessed with a conjunction of T-contrasts [SYN >SEM] across two groups of signers (deaf signers and hearing signers). For illustration, mean parameter estimates (arbitrary units ± SEM) at significant peaks are plotted separately for each condition. Results are overlaid on a coronal (upper panel) and a transverse slice (lower panel) of the mean structural image of all of the participants. Images are displayed at a threshold of $p < .001$ (uncorrected) with a spatial extent threshold of 10 voxels. Colour bars represent t-values. Coordinates are in Montreal National Institute (MNI) space. L = left, R = right, IPS = inferior parietal sulcus. See Table 4 for a list of regions depicted in this figure. See also Supplementary Fig. 5.

Table 4

Coordinates and statistics for the effects of syntactic violations. Coordinates in this table are reported if significant ($p < .05$) after correction over the whole brain. k represents the number of voxels when displayed at $p_{\text{(uncorrected)}} < .001$.

Area	k	p (FWE – corr)	Z-score	x	y	z
SYN vs CORR						
right supramarginal gyrus (area PFm)	137	<.011	4.88	57	−46	40
SYN vs SEM						
right inferior parietal sulcus (hIP3)	411	.020	4.77	39	−52	49
right supramarginal gyrus (area PF)		.023	4.73	48	−40	55
right supramarginal gyrus (area PFt)		.033	4.64	54	−34	55
right superior parietal lobule		.050	4.53	39	−37	37

language processing to generate predictions about low-level form-based features such as phonology (Gagnepain et al., 2012) and orthography (Dikker and Pylkkanen, 2011; Dikker and Pylkkänen, 2013; Kherif et al., 2011). Most pertinent to our study is the report of sensory processing effects for lexical-semantic prediction violations in written language: Dikker and Pylkkanen (2011) paired written words with either semantically congruent or incongruent preceding pictures and found that early visual responses were sensitive to whether or not a prediction for a specific word form was satisfied. Dikker and Pylkkänen (2013) explained these effects in terms of top-down modulation: Contextual cues induce increased activation in neuronal populations that encode the relevant representations and simultaneously suppress activity in neurons that represent irrelevant representations. This leads to enhanced processing costs within these regions when predictions are not satisfied and previously suppressed representations have to be reactivated while pre-activated representations that do not match the bottom-up input have to be suppressed.

Such an interpretation fits well with the hypothesis put forward by Almeida et al. (2015) that extensive SL experience leads to a visually driven forward model for human gestures that recruits primary visual areas. According to their view, perceptual tuning of early visual areas as a result of the life-long use of a SL leads to a more efficient processing of

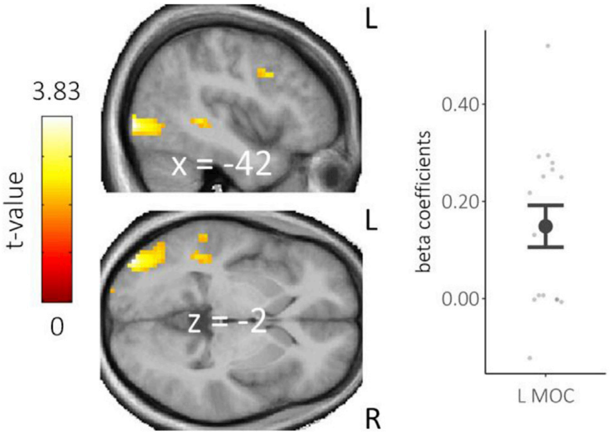

Fig. 6. Psychophysiological interaction (PPI) of the right supramarginal gyrus (SMG) showing stronger coupling during syntactic processing compared to semantic processing. For illustration, mean strength of connectivity (arbitrary units ± SEM) at significant peaks is plotted for the left MOC. Results are overlaid on sagittal (upper panel) and transverse slices (lower panel) of the mean structural image of all of the participants. Images are displayed at a threshold of $p < .001$ (uncorrected) with a spatial extent threshold of 10 voxels. Colour bars represent t-values. Coordinates are in Montreal National Institute (MNI) space. L = left, R = right, MOC = middle occipital cortex. See Table 5 for a list of regions depicted in this figure. See also Supplementary Fig. 6.

Table 5

Results of the functional connectivity (PPI) analyses seeded in the right supramarginal gyrus performed across the two groups of signers using a conjunction analysis. Coordinates in this table are reported if significant ($p < .001$) uncorrected over the whole brain with a spatial extent threshold of 10 voxels. Voxels marked with an asterisk survive whole-brain FWE correction at $p < .05$. *k* represents the number of voxels when displayed at $p_{\text{(uncorrected)}} < .001$.

Area	k	p (uncorrected)	Z-score	x	y	z
left middle occipital gyrus*	110	<.001	4.78	−42	−88	−2
right precentral gyrus	33	<.001	4.19	39	2	43
right middle frontal gyrus	94	<.001	4.13	48	32	22
right inferior frontal gyrus (pars triangularis)		<.001	4.09	48	17	25
left middle temporal gyrus	67	<.001	3.96	−45	−43	1
left middle temporal gyrus		<.001	3.76	−60	−43	4
left middle occipital gyrus	53	<.001	3.80	−27	−94	7
left middle occipital gyrus		<.001	3.63	−21	−103	4
left precentral gyrus	48	<.001	3.69	−36	2	34

Table 6

Coordinates and statistics for the interaction effects between hearing status and type of violation. Coordinates in this table are reported if significant ($p < .05$ FWE) after correction over anatomical regions of interest. *k* represents the number of voxels when displayed at $p_{\text{(uncorrected)}} < .001$.

Area	k	p (FWE – corr)	Z-score	x	y	z
right superior temporal gyrus	34	.005	4.16	63	−1	−11

complex articulatory body postures (Almeida et al., 2015). Thus, life-long use of a SL might lead to the development of finely tuned representations of SL relevant hand, face and body postures. Such representations would allow for a more precise prediction of SL relevant visual information and thus, would speed up SL comprehension.

In an fMRI study that compared the neural correlates of action observation in signers and non-signers, deaf signers showed increased activation in primary visual areas in response to non-linguistic actions compared to ASL signs (Corina et al., 2007). The authors suggested that this could reflect more automatic and efficient processing of visual linguistic information. Greater reliance on top-down processing would thus decrease the demands on early visual processing mechanisms during processing of visual linguistic information compared to non-linguistic information (Corina et al., 2007). Signers in our study may thus have used higher-level linguistic information of the preceding context to generate predictions about the upcoming articulatory hand and body postures, which led to increased processing costs in early visual areas when the predictions were not satisfied. Previous EEG/MEG studies have reported effects of lexical-semantic violations in the visual cortex for written language (Dikker and Pylkkanen, 2011) and in the auditory cortex for spoken language (Sohoglu et al., 2012). It thus seems that such predictions are a part of language comprehension but specific to the modality that the language is presented in.

While this interpretation fits nicely with the observed effects in early visual areas, it should be noted that most of the studies investigating semantic processing have not reported an involvement of early sensory areas (see Hagoort and Indefrey, 2014 for a review). The studies that observed such effects in early sensory areas (Dikker and Pylkkanen, 2011; Sohoglu et al., 2012) used paradigms that allowed a straightforward mapping between semantics and the visual/auditory form of the upcoming word. However, form estimates based on lexical-semantic predictions in sentential contexts are usually not as straightforward since a direct mapping between semantic properties and form properties usually does not exist. For example, the DGS signs for "snake" and "cat" both belong to the semantic category animal, but are unrelated in their form (hand configuration, movement, and handshape). In our study, the context does not set up for one particular sign, thus, the preactivation of only a single word form cannot be assumed. Manipulating the predictability of form properties in certain sentential contexts might be an interesting endeavour for future studies. This could shed some light on the role of early visual areas in SL processing.

Both groups of signers showed greater activation in the left IFG when processing sentences containing semantic violations compared to those containing syntactic violations (see Fig. 3). Increased activation of the left IFG for semantic violations compared to syntactic violations concurs

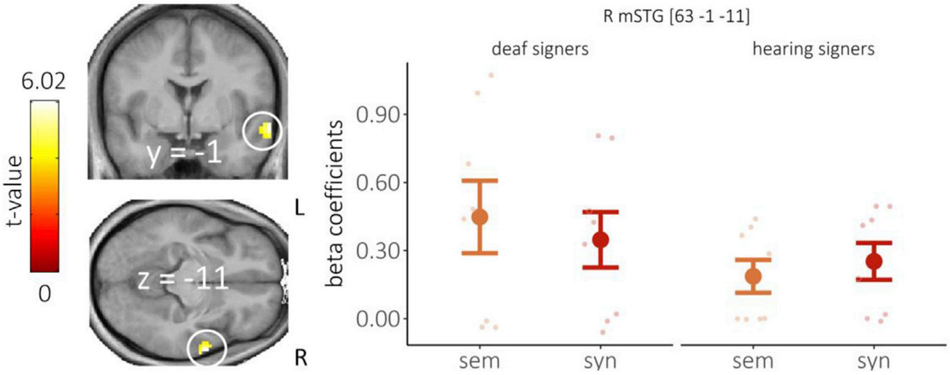

Fig. 7. Effects of hearing status in the right mSTC. Results are overlaid on a coronal (upper panel) and a transverse slice (lower panel) of the mean structural image of all of the participants. Images are displayed at a threshold of $p < .001$ (uncorrected) with a spatial extent threshold of 10 voxels. For illustration, mean parameter estimates (arbitrary units ± SEM) at significant peaks are plotted separately for each group and condition. Colour bars represent t-values. Coordinates are in Montreal National Institute (MNI) space. L = left, R = right, DS = deaf signers, HS = hearing signers, mSTC = middle superior temporal cortex. See Table 6 for a list of regions depicted in this figure.

with studies of written and spoken language processing that either directly contrasted these two types of violations (Dapretto and Bookheimer, 1999; Ni et al., 2000; Nieuwland et al., 2012; Rüschemeyer et al., 2006) or that compared sentences with high syntactic and high semantic processing demands (Borofsky et al., 2010; Rodd et al., 2010; Röder et al., 2002). Supporting evidence for the importance of the left IFG for language processing comes from studies that show that damage to this region can lead to aphasia for SpL (Wright et al., 2012) and SL (Atkinson et al., 2005; Poizner et al., 1987). Moreover, neuroimaging studies with healthy subjects have reported robust activations within the left IFG for spoken, written, and signed language processing (Emmorey et al., 2014; Inubushi and Sakai, 2013; MacSweeney et al., 2002; Moreno et al., 2017; see Price, 2012 for a review). According to models of language processing, the left IFG is thought to be involved in the retrieval and unification of lexical semantic information (Hagoort, 2005; Lau et al., 2008). This concurs with a more recent study by Inubushi and Sakai (2013) who showed that for SL, activation within this region can be modulated by the level of linguistic integration. Further evidence for the role of the left IFG in linguistic unification processes comes from studies that have shown a systematic activation increase in the left IFG as a function of constituent size for both spoken and signed languages (Moreno et al., 2017; Pallier et al., 2011). It thus seems that the left IFG processes semantic information independently of the perceptual modality of the language.

4.2. Syntactic processing

Both deaf and hearing signers showed greater activation in the right SMG when processing syntactic violations compared to correct sentences (see Fig. 4). The recruitment of the right SMG seems violation-specific, as we also observed increased activation of this area when sentences with syntactic violations were compared to sentences with semantic violations (see Fig. 5).

Lesion and neuroimaging studies have suggested that parietal regions, particularly in the right hemisphere, may play a crucial role in processing SL (Emmorey et al., 2014; see MacSweeney et al., 2008 for a review; Poizner et al., 1987). In an early lesion study, Poizner et al. (1987) reported that signers with damage to the right-hemisphere have intact language skills, despite having impaired visual-spatial skills. In contrast, patients with damage to the left hemisphere were impaired in a number of linguistic tasks and exhibited severe problems in the comprehension of syntactic relationships that are expressed through spatial mechanisms, although their visual-spatial skills were intact (Poizner et al., 1987). This picture seems to suggest a dissociation between visual-spatial abilities and linguistic abilities in SL users, which is surprising given the importance of spatial mechanisms in SL. However, Poizner et al. (1987) reported two cases with lesions in the right hemisphere who were not only impaired in their performance on visual spatial tasks, but also on tasks involving the comprehension of verb agreement. The authors noted that "[…] right-lesioned signers do not show comprehension deficits in any linguistic test, other than that of spatialized syntax" (Poizner et al., 1987, p. 154).

While most neuroimaging studies highlight the role of the left hemisphere in SL processing, several studies have reported extensive right hemispheric involvement as well. Most studies that reported right hemispheric recruitment during SL processing, used sentence-level material (Lambertz et al., 2005; MacSweeney et al., 2002, 2006; Neville et al., 1998; Newman et al., 2002; Sakai et al., 2005). This is similar to what has been reported in studies of SpL (Fedorenko et al., 2012), which seems to suggest that recruitment of areas in the right hemisphere is more likely when syntactic and discourse-level information is present (see Vigneau et al., 2011 for a review). What seems to be specific about right hemispheric recruitment during SL processing, however, is the extensive recruitment of parietal areas. Greater activation of parietal areas has been reported for SL compared to SpL for both production (Emmorey et al., 2014) and comprehension (Emmorey et al., 2014; MacSweeney et al., 2002). However, the specific role of parietal areas during SL processing has remained rather elusive.

The inferior parietal cortex comprises a number of subregions that serve different functional roles, such as perceptual and motor reorienting, episodic memory retrieval, language comprehension, number processing, and social cognition (Caspers et al., 2013). One of the subregions that showed increased activation for syntactic processing was area PFt within the right inferior parietal lobule (IPL, as revealed by the contrast [SYN vs SEM]). Area PFt seems to be involved during the observation and imitation of hand movements (see Caspers et al., 2010 for a review). Another subregion which showed increased activation for syntactic processing was area PFm within the right SMG (as revealed by the contrasts [SYN > CORR] and [SYN >SEM]). Previous studies have suggested an involvement of this area in spatial attention and perceptual reorienting. One task, which has reliably produced evidence for this region's role in perceptual reorienting, is the 'Posner cueing task'. During this task, a central cue indicates whether a following target stimulus will appear on the left or on the right side of a display. During the majority of the trials the target appears in the cued, i.e. the expected location. Activation of the right IPL tends to be greater when targets are presented in unexpected locations compared to when they are presented in expected locations (Arrington et al., 2000; Corbetta et al., 2000). These results are consistent with the idea that this region is involved in "[…] reorienting of attention when expectations are violated" (Cabeza et al., 2012, p. 339). Just like in the Posner task, the syntactic violations in our paradigm could be interpreted as violations of expectations about the spatial locations of the referents, which would require the participants to reorient their attention to the new, unexpected spatial location.

The results from the univariate analyses dovetail nicely with the results from our PPI analyses which showed an increased functional coupling of area PFm in the right hemisphere with middle occipital areas encompassing area hOc5 in the left hemisphere when signers processed syntactic violations compared to when they processed semantic violations. Area hOc5 has been suggested to be the cytoarchitectonic correlate of human motion-sensitive area V5/MT+. This result is particularly interesting in the light of previous reports of left-hemisphere dominance for motion processing in signers compared to right-hemisphere dominance in hearing non-signers (Bavelier et al., 2001; Bosworth and Dobkins, 1999). It has been suggested that the temporal coincidence of visual motion and linguistic information during SL processing results in increased motion sensitivity in the language-dominant left hemisphere, leading to lateralization differences for motion processing between signers and non-signers (Bavelier et al., 2001; Bosworth and Dobkins, 1999). Thus, the need to attend to the location and the movement of the hands in space could explain the enhanced activation of the right IPL and its increased functional connectivity with the left area MT when processing spatialized aspects of signed syntax.

4.3. Effects of hearing status on processing syntactic and semantic information

We observed an effect of hearing status in the right mSTC; this region was specifically responsive in deaf signers during semantic violations compared to syntactic violations, whereas the response in this region did not differ between the two conditions in hearing signers (see Fig. 7). When interpreting these effects, it should be taken into account that the deaf and hearing native signers of the present study not only differed with regard to their hearing status, but also in the frequency with which they used DGS and their proficiency. Hearing signers performed worse on the sentence judgement task than deaf signers. This result is in agreement with previous studies which found poorer performance in hearing compared to deaf native signers using similar tasks (MacSweeney et al., 2002; Neville et al., 1998). This group difference could be the result of an overall higher language proficiency in deaf compared to hearing native signers. In the self-ratings of their language proficiency, all deaf signers indicated their production and comprehension of DGS to be 1 on a scale of 1–4 (1 = excellent, 4 = not very good at all), whereas the hearing signers indicated their level of comprehension and production to be approximately 2 on average. Moreover, the deaf and hearing signers of the present study reported to have had different linguistic interactions with their parents during childhood. Whereas deaf signers indicated that they had always communicated in DGS with their parents, hearing signers indicated that they used a mixture of DGS, sign supported speech, and spoken language to communicate with their parents. This concurs with previous reports (see Singleton and Tittle, 2000 for a review). Moreover, the use of SL differed among the two groups in adulthood as well. Whereas all deaf participants indicated that they use DGS as their primary means of communication on a daily basis, most of the hearing participants reported that they use DGS at least once a week. While these differences are likely to have an effect on language processes and their underlying neural systems, previous studies on neural plasticity in deaf individuals have suggested that the effects observed in the right STC are more likely to be due to auditory deprivation rather than to SL proficiency (Fine et al., 2005; Twomey et al., 2017).

In hearing people, the STC has been associated with auditory processing and plays an important role during speech perception (DeWitt and Rauschecker, 2012). In deaf people this region has been shown to be activated to a greater extent than in hearing people in a number of different tasks that included both linguistic (Newman et al., 2015; Que et al., 2018; Twomey et al., 2017) and non-linguistic material (Almeida et al., 2015; Benetti et al., 2017; Bola et al., 2017; Fine et al., 2005; Finney et al., 2001; Que et al., 2018; Vachon et al., 2013), which has led some authors to argue that processing within the right STC is of perceptual nature (Twomey et al., 2017). While this might be true for posterior regions of the right STC, our results suggest that this is not the case for more anterior regions where we observed differential effects for semantic and syntactic processing. Given that our stimuli were matched for basic visual features and only differed in the linguistic information that was being presented, the differential effects for the two conditions in deaf signers are unlikely to reflect perceptual processing but rather point to processes that are more linguistic in nature.

Cardin et al. (2013) investigated how hearing status and SL experience shape the neural substrates of SL processing by comparing responses to SL material in deaf native signers and deaf and hearing non-signers. Within the right STC the authors reported that the effects of hearing status and SL experience were manifest in anatomically and functionally distinct cortical regions with the effect of hearing status mostly in the lateral portion of the right STC and the effect of SL experience extending more medially and anteriorly. However, at a more lenient threshold the two effects overlapped in some regions within the right STC, possibly indicating interactions between the two factors. Moreover, Cardin et al. (2013) assessed the effects of SL experience by comparing the group of deaf signers with deaf non-signers and hearing non-signers. Therefore, what they report as effects of SL could actually represent interaction effects of hearing status and SL. It could be hypothesized that the mid-anterior regions of the right STC are involved in linguistic processing in deaf but not in hearing signers. This interpretation dovetails with the results of our study that show differential recruitment of the right mSTC for different types of linguistic processing in deaf but not in hearing signers.

5. Conclusions

Taken together, our results indicate that linguistic processing in SL is supported by both modality-dependent and modality-independent brain regions and that hearing status affects the neural correlates of SL processing in the right STC. Semantic processing engages the left IFG, which concurs with studies of SpL suggesting modality-independent processing mechanisms, as well as primary visual areas, suggesting modality-dependent processing mechanisms. Syntactic processing engages the right inferior parietal lobule, which shows a strong coupling with the left area MT. This is taken to reflect the processing of the spatialized aspects of signed syntax. The right mSTC is differentially recruited for the two types of linguistic processing only in deaf signers, suggesting that when this region does not receive any auditory input, it participates in linguistic processing in the visual-manual modality.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.06.025.

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