



Published in final edited form as:

Brain Lang. 2021 December ; 223: 105044. doi:10.1016/j.bandl.2021.105044.

The neural correlates for spatial language: Perspective-dependent and -independent relationships in American Sign Language and spoken English

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Abstract

In American Sign Language (ASL) spatial relationships are conveyed by the location of the hands in space, whereas English employs prepositional phrases. Using event-related fMRI, we examined comprehension of perspective-dependent (PD) (*left, right*) and perspective-independent (PI) (*in, on*) sentences in ASL and audiovisual English (sentence-picture matching task). In contrast to non-spatial control sentences, PD sentences engaged the superior parietal lobule (SPL) bilaterally for ASL and English, consistent with a previous study with written English. The ASL-English conjunction analysis revealed bilateral SPL activation for PD sentences, but left-lateralized activation for PI sentences. The direct contrast between PD and PI expressions revealed greater SPL activation for PD expressions only for ASL. Increased SPL activation for ASL PD expressions may reflect the mental transformation required to interpret locations in signing space from the signer's viewpoint. Overall, the results suggest both overlapping and distinct neural regions support spatial language comprehension in ASL and English.

Keywords

fMRI; Spatial language; Sign language; Deaf; English

1. Introduction

Comprehending spatial language requires an interface between spatial cognition and the linguistic system (Landau & Jackendoff, 1993). Many spoken languages encode spatial relationships between a ground (reference) object and figure (located) object using categorical, closed-class morphemes, such as prepositions (e.g., *in, on, behind*) (Levinson, 2003). Left parietal cortex appears to be involved in processing non-linguistic, categorical spatial relationships in which the precise metric specification of the spatial configuration

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

is irrelevant and groupings of locations (e.g., variations of *above*) are treated as equivalent (Amorapanth et al., 2010; Kosslyn, 1987; Laeng, 1994; see Jager & Postma, 2003, for review). Further, both imaging and lesion studies have confirmed that left parietal cortex, particularly the supramarginal gyrus, is involved in producing and comprehending spatial prepositions, indicating that left parietal cortex may represent an interface between spatial cognition and language (e.g., Noordzij et al., 2008; Tranel & Kemmerer, 2004).

In contrast, sign languages typically encode spatial relationships with verbal classifier constructions rather than by lexical prepositions (Emmorey, 2003; Sandler & Lillo-Martin, 2006). In these constructions, the non-dominant hand typically represents the ground object, the dominant hand represents the figure object, and the spatial relationship is iconically depicted by how the hands are positioned in relation to each other (Emmorey, 1996). Classifier handshapes in these constructions are closed-class pronominal morphemes that specify the type of object (e.g., a person, a flat surface, etc.), but there are no morphemes that specify the locative relationship. Rather, signers must infer the spatial relationship between objects based on the arrangement of the two hands in signing space. Such constructions allow for a more gradient, less categorical, expression of the location of a figure object, such as height variations for *above* (Emmorey & Herzig, 2003). Processing this type of spatial language may rely on non-linguistic visual-spatial cognitive abilities, such that deaf signers who have visual-spatial processing deficits exhibit specific impairments in comprehending and producing spatial classifier constructions (Atkinson et al., 2002; Quinto-Pozos et al., 2013).

With respect to language production, several neuroimaging studies have shown that bilateral superior parietal cortex (extending into inferior parietal cortex) is engaged when signers produce classifier constructions in American Sign Language (ASL) that express spatial relationships, such as *in*, *on*, *left*, *right*, etc. (Emmorey et al., 2002, 2005, 2013). Lesion data also indicate bilateral involvement - signers with aphasia (left hemisphere damage) and signers with unilateral right hemisphere damage both produce errors when using classifier constructions (Atkinson et al., 2005; Emmorey et al., 1995; Hickok et al., 2009). In contrast, neuroimaging data for spoken languages suggests that the production of spatial prepositions primarily engages left parietal cortex (Damasio et al. 2001), and lesion data support these results. Speakers with left parietal damage (specifically, white matter underneath the inferior parietal operculum) make errors when naming spatial relations (Tranel & Kemmerer, 2004). Thus, the current evidence indicates that the production of locative expressions for sign language involves bilateral superior parietal cortex, but only left inferior parietal cortex for spoken language.

A possible explanation for this modality difference is that signers must map the perceived location of figure and ground objects onto a body-centered representation of the hands in signing space, whereas speakers must select a categorical, spatial morpheme to express the spatial configuration (Emmorey et al. 2013). The superior parietal lobule (SPL) is known to be involved in the on-line control and programming of reach movements to target locations in space (e.g. Glover, 2004) and in the control of visual spatial attention (e.g., Corbetta et al., 1995). Bilateral SPL may be recruited for the production of spatial classifier expressions

because of the visual-motor transformation that is required for signed, but not spoken languages.

However, it is unclear whether bilateral SPL is also engaged during the *comprehension* of spatial classifier constructions. Using fMRI, MacSweeney et al. (2002) compared neural activation for deaf users of British Sign Language (BSL) when comprehending “topographic” versus “non-topographic” BSL sentences; the task was to detect an occasional semantically anomalous sentence. Topographic sentences used signing space and/or the signer’s body to express spatial information, while non-topographic sentences did not. The contrast between these two sentence types revealed greater activation for the topographic sentences in left but not right parietal cortex. However, the topographic sentences did not focus specifically on spatial relationships and included a wide range of constructions. For example, English translations of the BSL sentences included: *The woman shaved her legs; I flew from London to Dublin; the woman handed the boy a cup; and the bouncer punched the man in the face*. It is possible that activation in right parietal cortex was not observed for the topographic sentences because only a handful of sentences required mapping the location of the hands in signing space to the location of figure and ground referents (e.g., *The cat sat on the bed*). In addition, Atkinson et al. (2005) found that BSL signers with unilateral right hemisphere damage were impaired in their ability to comprehend sentences that expressed spatial relationships with classifier constructions in comparison to healthy older control signers. Left-hemisphere damaged signers were also impaired, suggesting that comprehension of locative classifier constructions depends on functions of both hemispheres.

Newman et al. (2015) also failed to find activation in superior parietal cortex when ASL signers comprehended sentences that expressed location and motion information compared to a “backward/layered” control condition in which the sentence videos were played backward with three different videos superimposed. The experimental task was to decide whether a sentence matched a preceding video, and the control task was to determine whether during the movie, three hands had simultaneously had the same handshape. However, not all sentences expressed location information (e.g., some sentences described objects; see Supplementary Materials for Newman et al., 2015), and the visually complex baseline condition and spatial attention task may have swamped any parietal activation related to interpreting spatial relationships in the signed sentences. To date, no neuroimaging study to our knowledge has investigated what neural regions support comprehension of locative classifier constructions that specifically express spatial relationships.

In contrast, similar investigations have been conducted to examine the neural correlates for the comprehension of spatial prepositions in spoken languages. For example, using fMRI Noordzij et al. (2008) compared the comprehension of spatial expressions (*circle left of triangle*) and non-spatial expressions (*circle and triangle*) in which the task was to determine whether a first expression matched either a second written expression or a picture. The contrast between spatial and non-spatial conditions revealed greater activation in left, but not right, parietal cortex, specifically in the left supramarginal gyrus. However, Conder et al. (2017) suggested that a lack of activation in the right hemisphere may have occurred because neural activity associated with the pictures and with the decision process were also included

in the contrasts. Conder et al. (2017) argued that some of the inconsistencies regarding the role of right parietal cortex in comprehending spatial prepositions may occur because the reported analyses often include neural activations associated with task performance (e.g., processing a picture) together with activations associated with processing the spatial language under investigation. To circumvent this problem, Conder et al. (2017) used an event-related design in which participants decided whether auditorily presented spatial sentences (e.g., *The triangle is below the square*) or non-spatial sentences (e.g., *The triangle is smaller than the square*) matched a picture that only occasionally followed the sentence, and these latter trials were excluded from analysis. This study found that spatial sentences elicited more activation in the superior parietal lobule and precuneus bilaterally compared to non-spatial sentences describing size or color.

The present study adopted the design used by Conder et al. (2017) to compare comprehension of spatial and non-spatial sentences presented in ASL to deaf signers and in audiovisual English to hearing speakers. One goal was to determine whether bilateral superior parietal cortex was engaged for both language modalities, indicating a shared substrate for comprehending spatial language. A second goal was to examine whether there are neural differences when comprehending perspective-independent (topological) spatial relationships (e.g., *in, on, above, below*) compared to perspective-dependent (projective) relationships (e.g., *left of, right of, behind, in front of*). Typically, these types of spatial relationships have been mixed together in studies of the neural substrates for spatial language, but their comprehension may involve different cognitive processes.

Understanding perspective-independent (PI) expressions (e.g., *in, on*) does not depend upon the viewpoint of the addressee or the speaker/signer. The spatial relationship between the figure and ground objects is the same regardless of the position of the addressee or the speaker/signer. In contrast, to comprehend perspective-dependent (PD) spatial expressions (e.g., *to the left of, behind*), the addressee must consider the viewpoint of the speaker/signer (Levinson, 2003). PD expressions can encode a *relative* frame of references in which the viewer's perspective must be understood (e.g., *The triangle is behind the square*) or from an *intrinsic* frame of reference in which the front/back/left/right of the ground object must be understood (e.g., *The dog is in front of the house*). Using fMRI, Janzen et al. (2012) investigated the comprehension of relative and intrinsic PD sentences compared to non-spatial control sentences. The authors capitalized on the ambiguity of sentences like *The ball is behind the man* which could be interpreted from an egocentric perspective (from the perspective of the viewer/participant) or from an object-oriented perspective (i.e., based on the intrinsic features of the man, regardless of the viewer's perspective). Participants performed a written sentence-picture matching task with feedback regarding which frame of reference should be adopted when understanding the ambiguous sentences. Janzen et al. (2012) found that activation in the parahippocampal gyrus was associated with PD sentences interpreted using the intrinsic frame of reference, whereas activation in the right superior frontal gyrus and left superior parietal lobule was associated with sentences interpreted using the relative frame of reference. Janzen et al. (2012) suggested that the latter finding is consistent with the proposal that a frontal-parietal network is involved computing viewer-centered spatial coding (Committeri et al., 2004). In the present study, we examine unambiguous PD sentences that can be interpreted only from a relative frame of reference.

By convention, PD expressions in ASL, as in many sign languages, are expressed from the signer's perspective (Pyers et al., 2015). For example, as shown in Fig. 1A, to express "The box is to the left of the ball", the signer places a classifier handshape referring to the box on her left and another classifier handshape referring to the ball on her right. However, an addressee who is facing the signer perceives the 'box' classifier on the right and the 'ball' classifier on the left. Therefore, the addressee must perform a mental transformation (a 180° rotation along the horizontal plane) in order to understand this perspective-dependent spatial expression. Such a mental transformation is not required to comprehend the equivalent audiovisual expression in English and correctly perform the sentence-picture matching task (Fig. 1A). Recent research shows that the mental transformation required to comprehend PD classifier expressions in ASL is not automatic, is impacted by visual angle (longer comprehension times for 180° (face-to-face) than 90° (side) positioning of the addressee), and is cognitively demanding (Brozdowski et al., 2019). Further, non-linguistic visual-spatial perspective-taking skill predicts comprehension ability for PD classifier expressions in deaf adult ASL signers (Secora & Emmorey, 2020). These findings suggest that comprehension of PD expressions in ASL may draw on additional neural resources compared to comprehending PI expressions in ASL, which do not require such a mental transformation (see Fig. 1B). In particular, given the known role of parietal cortex in mental rotation and visual-spatial perspective-taking (e.g., Zacks, 2007), we predict greater parietal activation during the comprehension of PD sentences than PI sentences in ASL signers.

In sum, in this study we presented videos of ASL spatial sentences to deaf signers and videos of their English translations to hearing speakers who performed an occasional sentence-picture matching task. The spatial sentences expressed either perspective-independent (PI) or perspective-dependent (PD) information, and the control sentences described the color of the figure and ground objects. Our goals were to a) identify common neural substrates for comprehending spatial language across modalities and linguistic strategies (i.e. categorical morphemes vs. analogue depictions) and b) investigate whether the comprehension of PD and PI spatial expressions recruits distinct neural regions in either ASL signers or English speakers.

2. Methods

2.1. Participants

Fourteen deaf signers (8 female; mean age = 29.6; SD = 4.35 years) and 14 hearing English speakers (8 female; mean age = 26.3; SD = 6.7 years) participated in the study. All deaf signers were profoundly deaf and were exposed to ASL before age 6. All deaf participants reported using ASL daily with their families, friends, or colleagues in the workplace. All hearing participants were native speakers of English and had no or very minimal experience with ASL (e.g., limited to knowledge of the fingerspelled alphabet or a few signs). All participants in the study were right-handed and had normal or corrected-to-normal vision. None of the participants reported any current or past neurological or behavioral disorders (e.g., epilepsy or a learning disability). The groups did not differ in age, Welch two-sample *t*-test $t = 1.54$, $df = 22.8$, $p = .138$. All participants were recruited from the San Diego and Los

Angeles metropolitan areas. Informed consent was obtained from all participants according to procedures approved by the UCSD and SDSU Human Research Protection Programs.

2.2. Stimuli

For the spatial language conditions (PD and PI), we filmed 48 ASL sentences in which the model (a deaf female native signer) produced a sentence describing a spatial relationship between two different objects. Each spatial sentence contained nouns for two different objects from a set of five possible objects (vase, bowl, ball, candle, and box), and the sentence expressed one spatial relationship from eight possible spatial configurations (PD: *left, right, behind, in front of*; PI: *above, below, in, on*), with 24 sentences for each perspective type. Example sentences are illustrated in Fig. 1. In ASL, the location of the ground object is typically described before the figure object. All ASL spatial descriptions had the following serial linguistic structure:

1. A lexical noun referring to the ground object (e.g., BALL in Fig. 1A and 1B) was first produced followed by:
2. A classifier handshape for the ground object placed in space (e.g., CL-round-shape located on the left in Fig. 1A and high in signing space for Fig. 1B)
3. The lexical noun referring to the figure object (e.g., BOX and CANDLE for Fig. 1A and 1B, respectively)
4. A classifier handshape for the figure object was placed in space (e. g., CL-box-shape located on the right in Figure A and CL-tallshape located low in signing space in Fig. 1B) while the classifier handshape for the ground object was simultaneously placed in its previous location.

For the non-spatial language condition, we filmed 24 ASL sentences in which the signing model described two different objects sequentially using neutral space, i.e., the ASL nouns were not associated with specific locations in front of the signer (see Fig. 1C). Each sentence contained two different objects selected from the same five possible objects (vase, bowl, ball, candle, and box), and each object was described with one of five different colors (red, green, yellow, blue, white). The sentences in this condition contained no information about the spatial relationship between the objects.

We also created parallel sentences in spoken English, using identical descriptions of object locations and object colors for spatial and non-spatial conditions, respectively. We filmed a female native English speaker producing the English sentences. Examples of English sentences for the spatial and non-spatial conditions are “The candle is below the ball” and “The candle is yellow and the bowl is white” (see Fig. 1). A list of the English sentences (ASL translations) is provided in the Appendix. All signed and spoken sentences were video-recorded using 480p format (3:2 aspect ratio) and edited using Apple Final Cut Pro. All video clips of signed ASL and spoken English sentences were 4 s and 3 s in length, respectively.

2.3. fMRI design and procedure

In this rapid event-related fMRI study, we generated and optimized stimulus sequences for each participant with Optseq2 (<https://surfer.nmr.mgh.harvard.edu/optseq/>). This program created two runs (5 min 56 s each) of counterbalanced and jittered trials in which all three conditions have the same frequency and distribution optimized for maximum estimation of efficiency (Dale, 1999). Each condition (PD, PI, and non-spatial control sentences) were presented randomly 24 times across two scans. Each trial consisted of a 4 s video clip followed by a variable fixation period (4–10 s) as determined by the Opstseq2 program. Five sentences (out of 24) in each condition were followed by a 2 s ISI of fixation and then a 2 s presentation of a line drawing that either matched or did not match the description given in the sentence (50% matched).

The stimuli were projected onto a screen at the foot of the scanner bed, using an XGA video projector and MacBook Pro computer running PsyScope X Build 53 (psy.ck.sissa.it). Participants viewed the screen through a mirror placed atop the head coil and responded using an MRsafe Lumitouch 4-button response box (Photon Control; Burnaby, Canada), pressing one button for ‘yes’ (match) and another button for ‘no’ (mismatch) responses. Participants were instructed to decide whether the line drawings matched the spatial relationship or color descriptions in the preceding sentence. Participants were encouraged to respond as quickly and accurately as possible. Participants’ accuracy and response times (RTs) were recorded.

Instructions were given in ASL for the deaf signers and in spoken English for the hearing participants. Participants performed eight practice trials outside the scanner with different stimuli that were not presented in the experiment.

2.4. MR image acquisition

MRI data were collected at the Center for Functional MRI at the University of California, San Diego, on a 3-Tesla GE MR750 scanner equipped with an eight-channel head coil. For anatomical reference and spatial normalization, we acquired high-resolution structural images of each participant’s brain at the middle of the session using a T1-weighted Fast Spoiled Gradient-Recalled Echo sequence (FOV 256 mm, 256 × 256 matrix, 1 mm × 1 mm in-plane resolution, 176 1 mm thick sagittal slices, flip angle = 8°, inversion time = 600 ms). For functional images, we acquired 34 T2*-weighted, gradient-echo echo-planar (EPI) axial slices interleaved from inferior to superior, covering the whole brain, with a repetition time (TR) of 2000 ms, an echo time (TE) of 30 ms, flip angle = 77°, FOV = 224 mm, 64 × 64 matrix, 3.5 × 3.5 mm in-plane resolution, and 4.0 mm slice thickness (no gap). All structural and functional scans were visually inspected for any significant brain abnormalities or head movements (e.g., blurring, ghosting, or stripping).

We collected two functional scans (183 EPI volumes each) for ASL and two functional scans (167 EPI volumes each) for English. Five “dummy” volumes were added to the beginning of each functional scan to allow magnetization to reach steady state before stimulus presentation, and these were discarded during data preprocessing.

2.5. fMRI preprocessing and data analysis

All MRI data preprocessing was carried out using AFNI software (version AFNI_19.1.21; Cox, 1996; Ward, 2006). All EPI datasets were corrected for geometric distortion using a field map acquired during the same scanning session. We also conducted slice timing correction (*3dTshift*), head motion correction (*3dvolreg*), and spatial smoothing (6 mm full-width half-maximum Gaussian kernel) on all EPI datasets. All participants' EPI datasets were also aligned to their MRI structural images and registered to MNI-152 T1 standard space.

For first-level analyses, we conducted a regression analysis in AFNI (3dDeconvolve, 3dREMLfit) to estimate hemodynamic response function (HRF) for PD, PI, and non-spatial control sentences. Rigid-body motion (acquired from 3dvolreg), low-order Legendre polynomials (linear and quadratic terms), and regressors for the sentences with a target image were included as nuisance variables. We also used AFNI 3dFWHx (with -ACF option) to estimate the smoothness of participant datasets, which we subsequently used with 3dClustSIM for group-level multiple comparison correction.

For second-level analyses, we first conducted repeated-measures analyses separately for each language with AFNI's 3dLME. All spatial and control sentence contrasts were conducted with the statistical maps thresholded to $p < 0.05$ (corrected for multiple comparisons) using $p < .001$ and minimum cluster size set to 12 ($3.5 \times 3.5 \times 4$ mm) voxels as determined by 3dClustSim using group averaged FWHMx (-acf) outputs.

We also performed direct language contrasts (ASL vs. English) on PD minus control sentences and on PI minus control sentences using linear mixed-effects analysis with AFNI's 3dLME. There is one caveat that should be noted in the interpretation of the direct language contrasts; the stimulus lengths for the ASL and English sentences were 4 s and 3 s respectively. The differences (e.g., PD minus control sentences from each language) should cancel out the effect of stimulus length, making the language contrasts comparable. However, the possible effect of stimulus length differences on the language contrasts cannot be completely ruled out.

3. Results

3.1. Behavioral results

The accuracy and response time data for the sentence-picture matching task are presented in Table 1. One deaf and two hearing participants' behavioral data had to be excluded due to technical problems in data acquisition. For response time (RT), a linear mixed-effects model (with participants as random intercepts) indicated no group difference, $F(1,23) = 2.2$, $p = .15$ nor interaction between group and sentence condition, $F(2,46) = 0.86$, $p < .43$. However, there was a main effect of sentence condition, $F(2,46) = 11.7$, $p < .0001$. Post hoc comparisons of the sentence conditions using simultaneous tests for general linear hypotheses (R package 'multcomp') revealed that the RT for perspective independent (PI) sentences was significantly faster than either perspective dependent (PD) sentences, $Z = -3.38$, $p = .002$ or the non-spatial control sentences, $Z = 4.68$, $p < .0001$. There was no difference in RTs between PD and control sentences, $Z = 1.29$, $p = .39$.

There was no significant difference in response accuracy between ASL signers and English speakers, $F(1,72) = 0.0006$, $p = .94$, nor significant interaction between group and sentence conditions, $F(2,72) = 1.56$, $p = .22$. The difference in accuracy across the conditions, however, was significant, $F(2,72) = 5.58$, $p = .006$. Post hoc analyses revealed that the responses for non-spatial control sentences were less accurate than for the PD sentences, $Z = 2.43$, $p = .04$, and the PI sentences, $Z = 3.19$, $p = .004$. The difference in the response accuracy between PD and PI sentences was not significant, $Z = 0.76$, $p = .73$.

3.2. fMRI results

We conducted second-level whole-brain analyses, comparing brain activation for spatial language types (PD and PI) and the non-spatial language control. All imaging results were significant at $p < 0.05$ (thresholded with a familywise correction using the uncorrected $p = 0.001$ and minimum cluster size of 588 mm^3 as determined by AFNI's 3dClustSim). For illustration clarity, only brain activation up to 25 mm beneath the cortical surface is shown in the Figures.

3.2.1. Regions of activation for perspective-dependent (PD) spatial relationships

—Fig. 2 presents contrast maps of brain regions that were significantly active for PD spatial language when contrasted with the non-spatial language control. Brain images from the ASL group show bilateral activity in parietal and occipital cortices, left superior frontal gyrus, right precentral gyrus, and middle frontal gyrus. Additional regions of brain activation that are not shown in Fig. 2 can be found in Table 2. Submaximal peaks within large clusters as determined by AFNI's 3dExtrema program, with a minimum 10-mm distance between peaks, are also included in Table 2. Brain images from English speakers show bilateral activity in the superior frontal gyrus and superior parietal lobe (see Fig. 2, bottom; Table 3).

The only brain regions where ASL signers showed greater activity for the non-spatial sentences were in the right superior temporal gyrus and left insula (Table 2). English speakers also showed greater bilateral activation in superior temporal gyrus and left medial superior frontal gyrus for non-spatial sentences (Table 3).

3.2.2. Regions of activation for perspective-independent (PI) relationships

—Fig. 3 presents contrast maps of brain regions activated for PI spatial language when contrasted with the non-spatial language control. Brain images from ASL signers show bilateral activity in superior parietal lobules, right middle temporal gyrus, left middle occipital gyrus, right precentral gyrus, left superior frontal gyrus, right posterior superior temporal gyrus. A cluster of activity in the right parahippocampal gyrus is not shown in Fig. 3 but is listed in Table 2. Brain images from English speakers show bilateral activity in precentral gyrus / superior frontal gyrus, left superior parietal lobule, left inferior parietal lobule, right inferior parietal lobule, left posterior middle temporal gyrus, and right anterior middle temporal gyrus (Fig. 3, bottom). Clusters of neural activation in left medial temporal pole and cerebellum VII are not shown in Fig. 3 but are listed in Table 3.

ASL signers showed greater bilateral activation for non-spatial sentences in the insula, left medial belt complex, and right cuneus (Table 2). English speakers showed greater activation

in superior temporal gyrus and left medial superior frontal gyrus for non-spatial sentences (Table 3).

3.2.3. Direct contrast between PD and PI sentences—The whole-brain PD and PI contrast map for ASL ($p < .05$, corrected) shows greater bilateral activity in precuneus / superior parietal lobules for PD sentences and greater activity in medial superior frontal gyrus for PI sentences (Fig. 4). There was no significant difference in neural activation between spatial language types for spoken English.

3.2.4. Conjunction maps of PD and PI sentences for ASL and English—We performed conjunction analyses, using the minimum statistic compared to the conjunction null method (Nichols et al., 2005), using maps from the perspective-dependent minus the non-spatial control and perspective-independent minus non-spatial control (all maps were $p < .05$, corrected) to identify the common neural regions for these spatial language types across languages (ASL and spoken English) (Table 4). For PD sentences, common activity across languages was found in bilateral superior frontal gyrus and parietal lobes (Fig. 5, top). For PI sentences, common neural activity across languages was found in bilateral superior frontal gyrus, left superior parietal lobe, left supramarginal gyrus, left middle temporal gyrus, and right middle occipital gyrus (Fig. 5, bottom).

3.2.5. Direct contrast between ASL and English—We also conducted whole-brain language contrasts (ASL vs. English) for PD minus control sentences and for PI minus control sentences (Fig. 6), although we note that this analysis should be interpreted with caution, given the length difference between the spoken and signed sentences. The ASL vs English PD contrast revealed greater bilateral activity for ASL signers in inferior frontal gyrus, caudate nucleus, middle frontal gyrus, and superior parietal lobe. ASL signers also showed greater activity in left precentral gyrus, middle occipital gyrus, and cerebellum (Table 5). There were no regions of greater activity for English speakers for PD sentences.

The ASL vs. English contrast for PI sentences showed greater activity for ASL signers in superior parietal lobe bilaterally, left inferior parietal lobe, left inferior occipital gyrus, right middle frontal gyrus, right middle temporal gyrus, and right occipital gyrus. English speakers showed more activity than ASL signers for PI sentences in bilateral insula and left parahippocampal gyrus.

4. Discussion

To our knowledge, this is the first study to investigate the neural regions engaged during the comprehension of expressions that specifically encode spatial relationships in a signed language. The results indicate that, like the production of ASL locative classifier constructions (Emmorey et al., 2002; 2005; 2013), comprehension of such constructions engages the superior parietal lobule (SPL) bilaterally. Thus, recruitment of SPL during sign production is not due solely to the articulatory requirements of placing the hands in space to depict the spatial relationship between figure and ground objects. We suggest that SPL is engaged during both comprehension and production because this region supports the interface between spatial cognition and spatial language (Conder et al., 2017). Importantly,

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Amorapanth et al. (2010) found that bilateral SPL was more engaged when people judged whether two pictures depicted the same spatial relationship (e.g., *in*, *behind*) between two different objects compared to when they judged whether the pictures contained the same objects, indicating that bilateral SPL plays a specific role in interpreting non-linguistic, but categorical spatial relationships. Thus, SPL may be involved in the computation that maps between a linguistic representation and a non-linguistic mental representation of the spatial configuration of objects. Such a computation likely involves several functions that are associated with superior parietal cortex, e.g., attention to spatial configurations (Molenberghs et al., 2007), spatial updating and coding different elements in space (Creem & Proffitt, 2001), and supramodal representations of spatial information (Struiksma et al., 2009).

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Supporting this hypothesis, the ASL-English conjunction analysis revealed that comprehension of spatial expressions in both signed and spoken language engaged SPL. As can be seen in Fig. 5, the shared system for spatial language comprehension included the dorsal fronto-parietal network, which is part of the core system for spatial processing identified in the recent *meta*-analysis by Cona and Scarpazza (2019). Specifically, these authors suggested that the dorsal fronto-parietal regions of the spatial processing network are involved in directing attention to internal representations of topographic spatial maps in response to behavioral demands. Comprehending either ASL or English spatial expressions involves creating an internal representation of the spatial location of figure and ground elements, despite distinct linguistic structures and modalities.

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The conjunction analysis also revealed that SPL activation was bilateral for perspective-dependent (PD) sentences, but left-lateralized for perspective-independent (PI) sentences. Consistent with this result, the ASL direct contrast between these two perspective types revealed greater activation in right SPL for PD sentences (Fig. 4), while the English direct contrast did not reveal a significant difference between the two types of sentences. However, the null result for English should be viewed with caution given our relatively small participant sample and given the results of the separate contrasts with non-spatial English control sentences. These contrasts revealed activation in right SPL for PD sentences (Fig. 2, bottom), but only left SPL activation for PI sentences (Fig. 3, bottom). Together, these findings suggest that right SPL may be particularly involved in interpreting spatial language that encodes relationships between objects from a relative point of view.

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The conjunction analysis for the PI sentences revealed additional shared activation in left middle temporal gyrus (MTG) and in the inferior parietal lobule, specifically in the left supramarginal gyrus (SMG). The spatial configurations described by PI sentences focus specifically on the topographic arrangement (*in*, *on*, *above*, *below*) between figure and ground objects, without regard to viewpoint. Previous studies have found that left SMG is engaged when speakers comprehend or produce these prepositions and damage to this region impairs their comprehension (Damasio et al., 2001; Struiksma et al., 2011; Tranel & Kemmerer, 2004). Following Kemmerer (2006), we suggest that the left SMG supports the representational dimensions of the spatial concepts encoded by these prepositions and by the parallel ASL classifier constructions, i.e., containment (*in*), surface contact and support (*on*), and adjacency relations (*above*). The inferior parietal lobule (IPL) and MTG are part

of the semantic network for language (e.g., Binder et al., 2009; Montefinese et al., 2020), and IPL also represents information about object location and shape for object-directed actions (Culham & Valyear, 2006), which may allow for the abstraction of categorical spatial concepts (Amorapanth et al., 2012). We suggest that these regions may be involved in interpreting and representing the spatial relationships conveyed by topographic spatial expressions, regardless of language modality.

The direct contrast between ASL and English revealed that the dorsal frontal-parietal network was more engaged for ASL signers than for English speakers when comprehending PD sentences (compared to non-spatial control sentences). This finding supports our hypothesis that understanding PD sentences in ASL requires additional neural computations due to the mental transformation required to convert observed locations in signing space into a mental representation of the locations from the signer's perspective (see Fig. 1A). Such a mental transformation is not required to comprehend English sentences – there is no conflict between the speaker and addressee viewpoints for perspective-dependent terms (e.g., right, left) in this sentence-picture matching paradigm.

When comprehending both PD and PI sentences (vs. control sentences), ASL signers also recruited posterior MTG (more extensive in the left hemisphere) to a greater extent than when English speakers comprehended these sentence types. One possible explanation for this difference is that for both the PD and PI sentences, ASL signers had to track where the signer placed the classifier handshapes in signing space, which may have recruited motion-sensitive regions (MT+; see also McCullough et al., 2012). For the non-spatial control sentences, there was no need to track where then hands moved in space because movements toward a location in neutral space (or on the body) did not carry meaning. Similarly, MacSweeney et al. (2002) found greater activation in bilateral posterior MTG (L > R) for BSL topographic sentences compared to non-topographic sentences. As in our study, where the signer's hands moved in signing space for the BSL topographic sentences carried meaning, but not for the non-topographic sentences.

In summary, comprehending spatial language in both signed and spoken languages requires an interface between language and cognitive systems involved in the construction and maintenance of visuospatial representations. The dorsal visual “where/how” pathway has long been known to support these processes in non-linguistic domains (Kravitz et al., 2011; Mishkin et al., 1983). Our findings indicate that bilateral SPL is recruited when either signers or speakers comprehend spatial sentences that are perspective-dependent, but signers engage these regions to a greater extent. We hypothesize this difference between languages is due to the additional computations needed to comprehend these sentences in ASL (Brozdowski et al., 2019). Comprehension of sentences that express perspective-independent topological spatial relationships also recruit this dorsal visual pathway for both languages, but neural activation is more left-lateralized and includes left SMG, as well as left MTG. We hypothesize that this temporo-parietal network in part supports the representational semantics of topological spatial expressions (e.g., containment, support, adjacency). Overall, our findings indicate that a) bilateral parietal cortex is engaged during comprehension of ASL spatial expressions, and not just during their production (Emmorey et al., 2002; 2005;

2013) and b) there is substantial overlap in neural regions that support comprehension of spatial language in ASL and English, despite the differences in modality.

Acknowledgments

The authors would like to thank all participants who took part in this study. This research was supported by a grant from the National Institutes of Health (R01 DC010997).

Appendix

Appendix A.

List of English sentences (ASL translations) in each condition

Perspective-Independent

- The vase is above the box.
- The candle is above the bowl.
- The bowl is above the vase.
- The vase is above the ball.
- The ball is above the candle.
- The candle is above the box.
- The candle is above the ball.
- The ball is above the vase.
- The candle is below the vase.
- The ball is below the box.
- The ball is below the bowl.
- The vase is below the box.
- The bowl is below the vase.
- The box is below the ball.
- The candle is below the bowl.
- The vase is below the candle.
- The ball is on top of the box.
- The bowl is on top of the box.
- The candle is on top of the bowl.
- The vase is on top of the bowl.
- The candle is in the box.
- The vase is in the box.
- The ball is in the bowl.
- The box is in the bowl.

Perspective-Dependent

- The bowl is to the right of the candle.
- The box is to the right of the vase.
- The candle is to the right of the ball.
- The bowl is to the right of the vase.
- The ball is to the right of the box.
- The vase is to the right of the bowl.
- The ball is to the left of the box.

The box is to the left of the candle.
 The bowl is to the left of the candle.
 The box is to the left of the bowl.
 The candle is to the left of the vase.
 The vase is to the left of the ball.
 The vase is in front of the box.
 The ball is in front of the candle.
 The bowl is in front of the vase.
 The box is in front of the bowl.
 The candle is in front of the box.
 The bowl is in front of the ball.
 The box is behind the ball.
 The vase is behind the ball.
 The candle is behind the bowl.
 The bowl is behind the vase.
 The ball is behind the candle.
 The vase is behind the box.

Non-Spatial sentences

The vase is yellow and the box is green.
 The bowl is yellow and the vase is green.
 The vase is white and the ball is yellow.
 The ball is yellow and the vase is orange.
 The box is orange and the ball is red.
 The vase is green and the ball is red.
 The bowl is red and the vase is green.
 The ball is red and the box is yellow.
 The vase is green and the candle is white.
 The candle is red and the bowl is yellow.
 The box is green and the ball is yellow.
 The ball is orange and the candle is blue.
 The box is white and the bowl is blue.
 The candle is orange and the box is green.
 The candle is orange and the bowl is blue.
 The vase is white and the bowl is orange.
 The bowl is white and the candle is yellow.
 The box is yellow and the candle is white.
 The box is blue and the bowl is orange.
 The ball is yellow and the box is red.

Perspective-Independent

The candle is blue and the box is green.
 The candle is yellow and the ball is green.
 The vase is red and the bowl is white.
 The bowl is orange and the vase is yellow.

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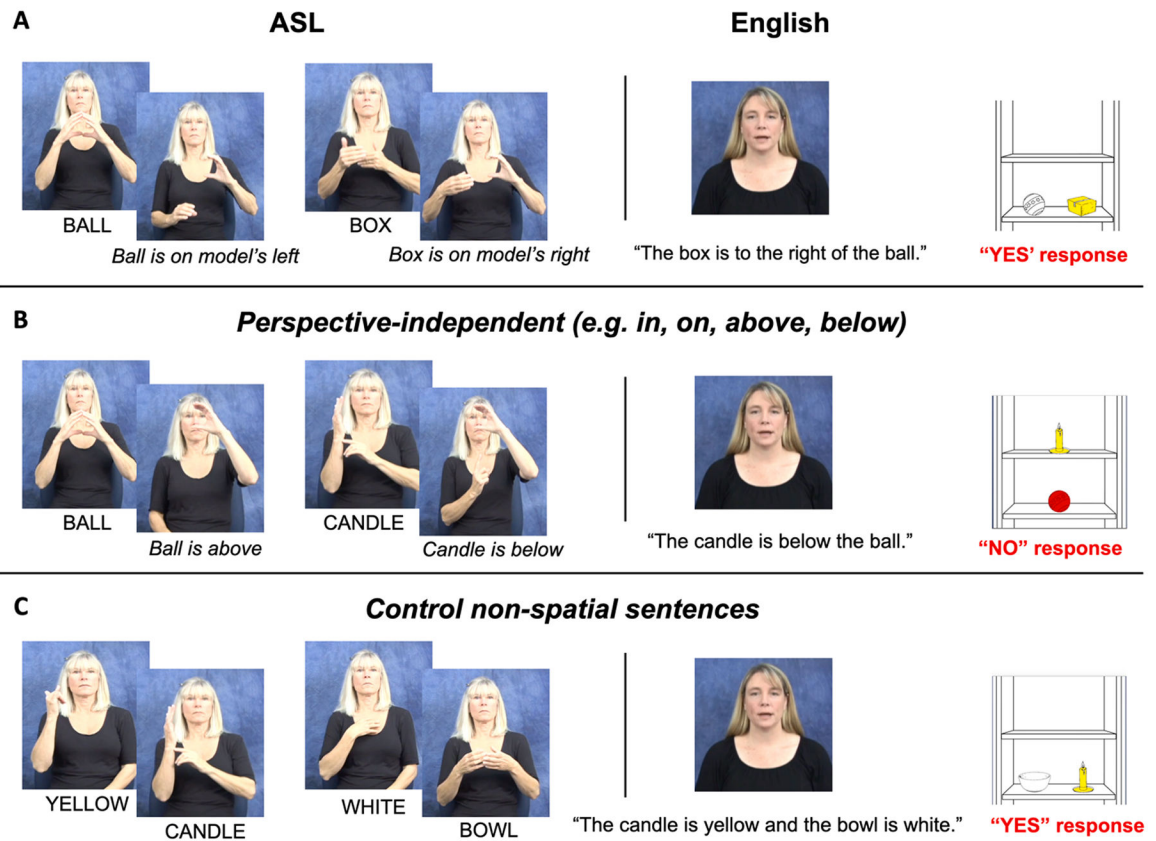
Perspective-dependent (e.g., left, right, front, behind)

Fig. 1. Examples of sentence-picture matching trials in ASL and English for A) Perspective-dependent spatial expressions, B) Perspective-independent spatial expressions and C) Non-spatial control sentences.

Perspective-dependent vs. Non-spatial control sentences

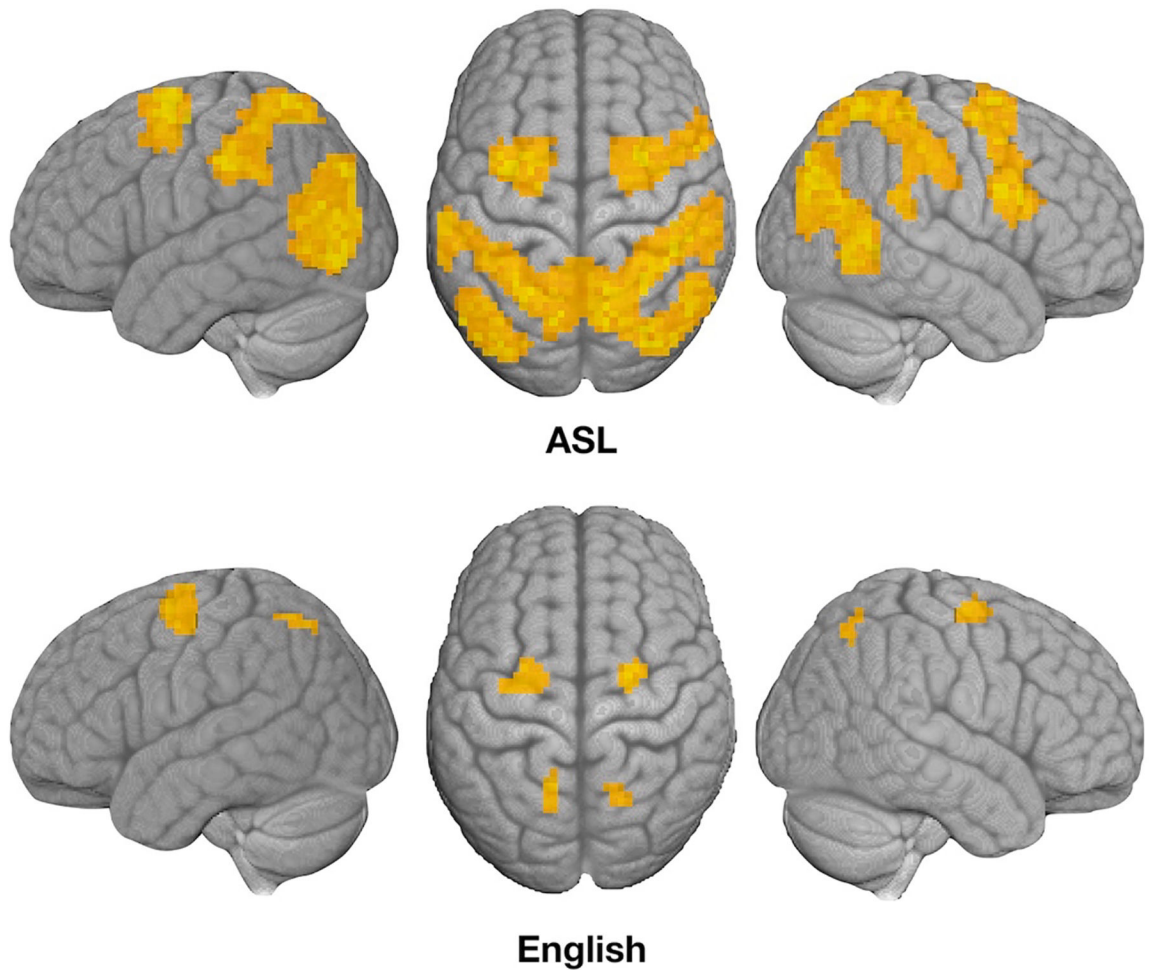


Fig. 2. FWE-corrected statistical maps for each language showing significant regions of brain activation up to 25 mm beneath the cortical surface of a template brain for the contrast between perspective-dependent spatial sentences and non-spatial control sentences. Orange denotes greater activation for perspective-dependent sentences.

Perspective-independent vs. Non-spatial control sentences

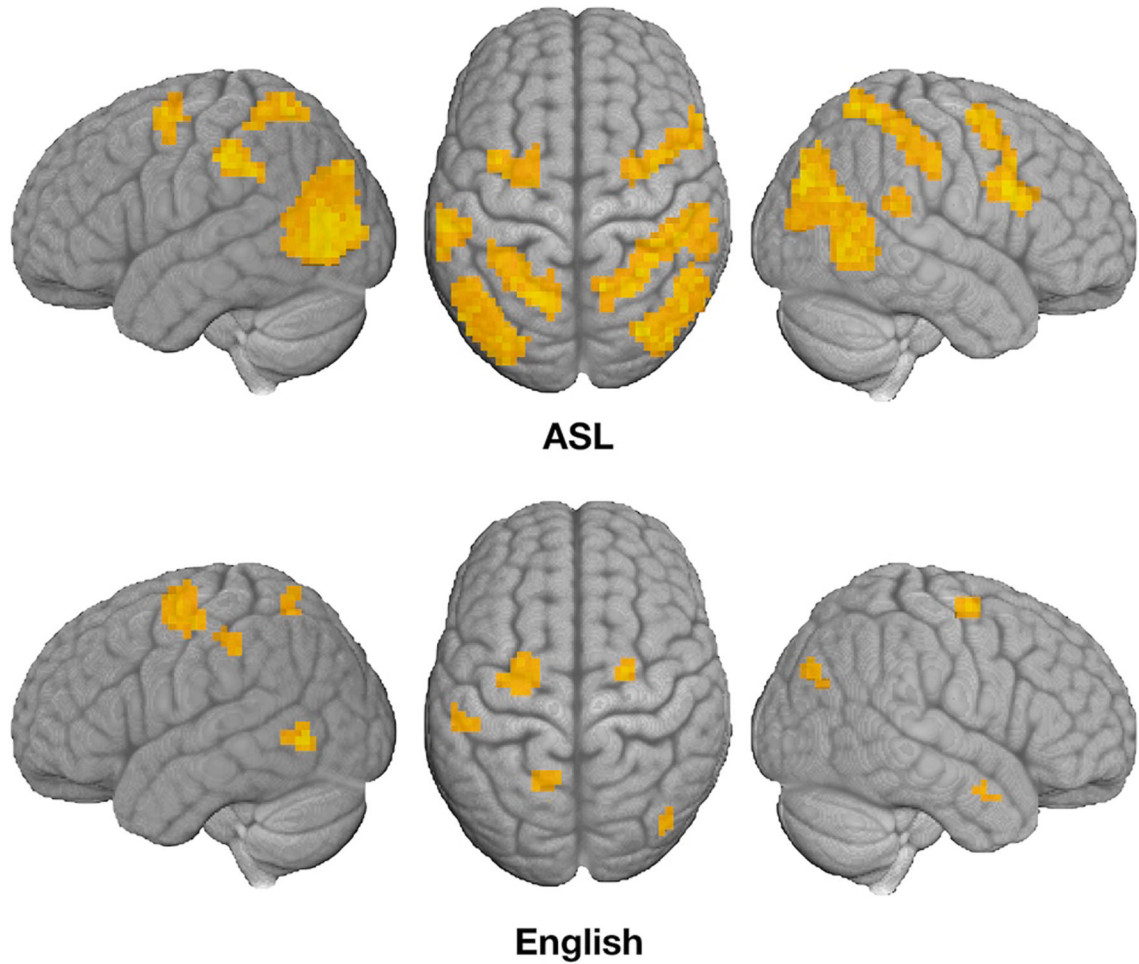


Fig. 3. FWE-corrected statistical maps for each language showing significant regions of brain activation up to 25 mm beneath the cortical surface of a template brain for the contrast between perspective-independent spatial sentences and non-spatial control sentences. Orange denotes greater activation for perspective-independent sentences.

Perspective-dependent vs. Perspective-independent sentences

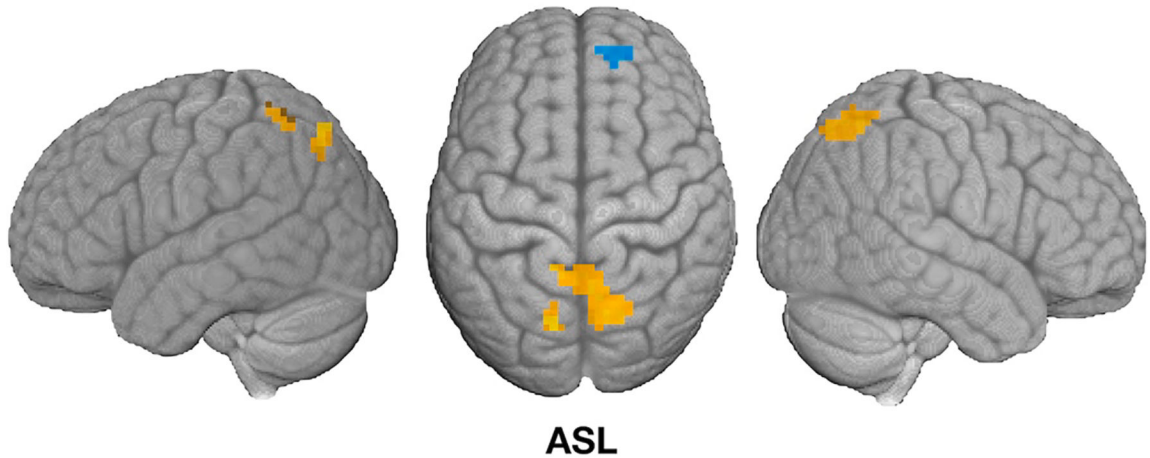
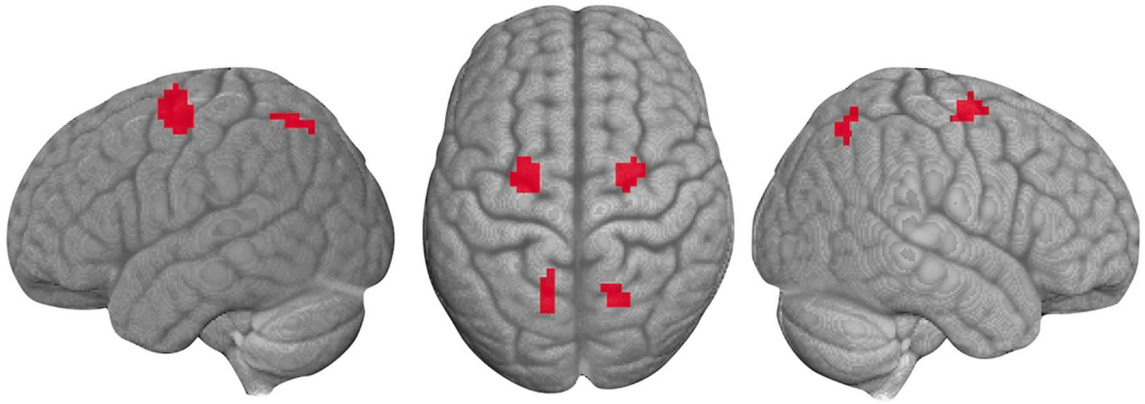


Fig. 4. FWE-corrected statistical maps (projected onto a template brain) showing regions of significant activation up to 25 mm beneath the surface for the direct contrast between perspective-dependent and perspective-independent spatial sentences in ASL. Orange denotes greater activation for perspective-dependent sentences, and cyan indicates greater activation for perspective-independent sentences. The direct contrast between these sentence types in English revealed no significant differences in cortical activation.

Language conjunction for perspective-dependent sentences



Language conjunction for perspective-independent sentences

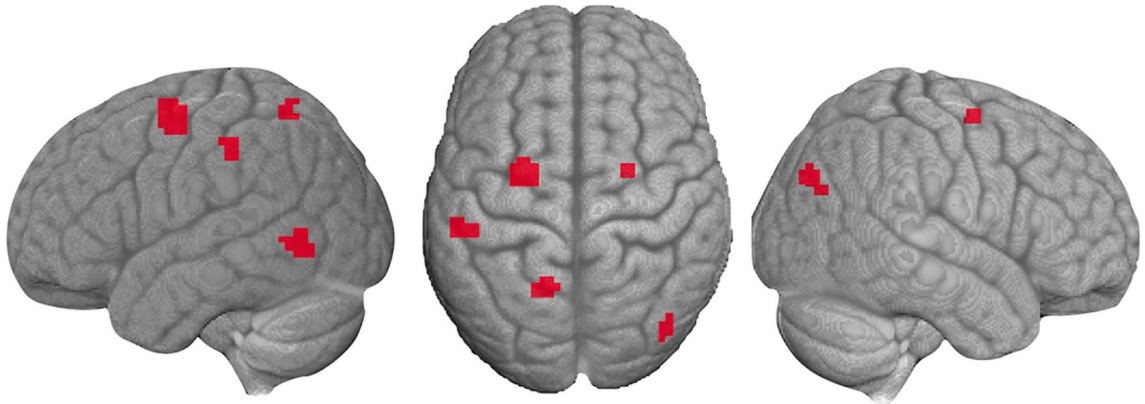


Fig. 5.

Conjunction maps projected onto a template brain, showing overlapping regions of activation for ASL and English for perspective-dependent spatial expressions and perspective-independent spatial expressions (each condition vs. its baseline).

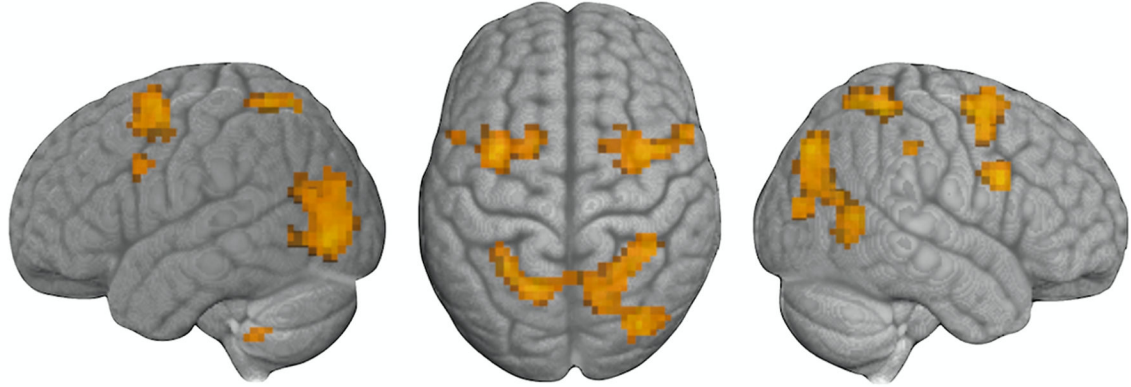
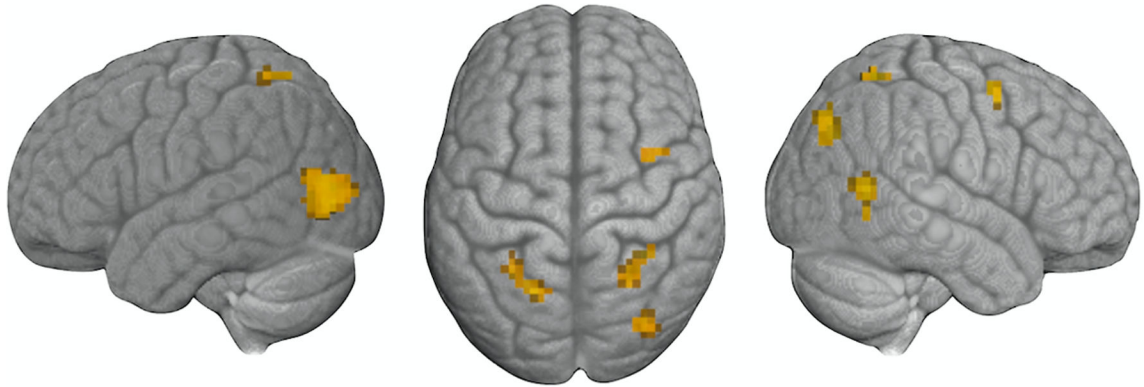
Language Contrast for Perspective Dependent Sentences: ASL > English**Language Contrast for Perspective Independent Sentences: ASL > English**

Fig. 6. FWE-corrected statistical maps from the language contrasts (ASL vs. English) for perspective-dependent and perspective-independent sentences (vs. non-spatial control sentences). Only significant differences of brain activation up to 25 mm beneath the cortical surface of a template brain are shown.

Table 1

Response time (ms) and accuracy (%) for the sentence-picture matching task for each group. Standard deviations are in parentheses.

	ASL signers		English speakers	
	RT	Accuracy	RT	Accuracy
Perspective Dependent	1701 (720)	81.4 (15)	1952 (505)	86.7 (19)
Perspective Independent	1473 (661)	85.7 (18)	1824 (349)	90.0 (13)
Non-Spatial Control	1704 (667)	77.1 (22)	2086 (355)	66.7 (17)

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Table 2

Second level contrasts between Perspective-Dependent (PD), Perspective-Independent (PI), and the non-spatial control sentences for ASL. Submaximal peaks are listed in italics.

Contrast	Brain region	MNI coordinates			Voxels	Z score
		X	Y	Z		
PD > Control	L Anterior insula	-33	29	-1	2615	6.2
	R Anterior insula	26	26	-8	1586	4.38
	L Caudate nucleus	-5	5	9	686	3.87
	R Caudate nucleus	9	12	6	1115	4.43
	R Precentral gyrus	54	8	30	21,995	8.67
	<i>Middle frontal gyrus</i>	33	-2	62		8.31
	L Superior frontal gyrus	-23	-2	58	13,892	9.15
	Parietal - Occipital Cortex				137,800	
	<i>L Supramarginal gyrus</i>	-58	-30	41		6
	<i>L Anterior IPS</i>	-47	-34	41		6.22
	<i>L Anterior IPS</i>	-37	-41	48		6.52
	<i>L Superior parietal lobule</i>	-16	-62	58		12.615
	<i>L Intraparietal sulcus</i>	-16	-65	44		7.01
	<i>L Angular gyrus</i>	-33	-76	27		5.73
	<i>L MT+</i>	-40	-76	9		7.77
	<i>R Middle occipital gyrus</i>	-44	-76	-1		8.24
	<i>R Superior parietal lobule</i>	33	-37	48		9.366
	<i>R Superior parietal lobule</i>	33	-44	58		9.703
	<i>R Superior parietal lobule</i>	26	-55	65		8.639
	<i>R Middle temporal gyrus</i>	54	-55	6		8.446
	<i>R Precuneus</i>	9	-58	58		7.989
	<i>R Precuneus</i>	19	-62	27		5.769
	<i>R Precuneus</i>	16	-69	41		6.085
<i>R Middle temporal gyrus</i>	40	-69	23		6.979	
<i>R Intraparietal sulcus</i>	30	-76	41		10.438	
<i>R Middle occipital gyrus</i>	40	-79	27		7.876	
R Parahippocampal gyrus	33	-34	-12	1072	5.18	
L Posterior cingulate cortex	-5	-44	27	729	4.34	
L Cerebellum VIII	-30	-37	-47	3902	5.89	
R Cerebellum VI	37	-44	-33	515	3.84	
Control > PD	L Insula	-33	-9	16	515	4.16
	R Superior temporal gyrus	54	-20	2	3773	5.5
PI > Control	R Precentral gyrus	54	8	30	8318	6.7
	L Superior frontal gyrus	-23	-2	55	4716	5.81
	R Superior temporal gyrus	61	-37	20	1329	5.2
	L Superior parietal lobule	-16	-62	58	16,850	9.53
	R Superior parietal lobule	33	-44	58	16,250	7.92

Contrast	Brain region	MNI coordinates			Voxels	Z score
		X	Y	Z		
	L Middle occipital gyrus	-40	-76	9	22,381	8.45
	<i>L Middle occipital gyrus</i>	-44	-76	-1		7.67
	<i>L Middle occipital gyrus</i>	-47	-62	-1		6.91
	R Middle temporal gyrus	54	-55	6	22,424	8.93
	<i>R MT+</i>	44	-58	-1		7.18
	<i>R Middle temporal gyrus</i>	44	-65	20		5.98
	<i>R Inferior parietal gyrus</i>	40	-79	27		6.66
	R Parahippocampal gyrus	33	-37	-12	515	4.6
Control > PI	L Insula	-30	8	20	557	-3.92
	R Insula	40	-20	2	2230	-4.5
	L Medial belt complex	-40	-30	2	557	-3.99
	L Medial belt complex	-37	-44	9	1158	-4.08
	R Cuneus	5	-86	20	1201	-5.04
PD > PI	L Putamen	-23	22	6	900	4.62
	R Putamen	19	15	-5	1243	3.96
	R Precuneus	9	-58	58	4245	4.71
	<i>L Precuneus</i>	-6	-51	50		4.15
	R Cuneus	19	-65	30	815	4.14
	L Superior parietal lobule	-12	-72	51	643	4.89
	L Calcarine gyrus	-16	-65	13	3902	4.37
	<i>R Calcarine gyrus</i>	11	-65	8		4.04
	L Cerebellum(VIII)	-44	-48	-50	643	4.23
PI > PD	R Medial sup. frontal gyrus	12	54	44	943	4.03

Table 3

Second-level contrasts between Perspective-Dependent (PD), Perspective-Independent (PI), and the non-spatial control sentences for English.

Contrast	Brain region	MNI coordinates			Voxels	Z score
		X	Y	Z		
PD > Control	L Superior frontal gyrus	-23	-2	62	4030	4.86
	R Superior frontal gyrus	23	-6	62	1243	5.1
	L Superior parietal lobule	-12	-58	58	686	4.36
	R Superior parietal lobule	19	-65	51	686	3.95
Control > PD	L Medial superior frontal gyrus	-5	5	65	1715	4.96
	L Superior temporal gyrus	-61	-23	2	2873	4.57
	R Superior temporal gyrus	54	-20	-1	2358	4.55
PI > Control	L Medial temporal pole	-37	8	-33	1458	5.16
	R Middle temporal gyrus	47	8	-26	643	4.04
	R Superior frontal gyrus, SMA	23	-6	62	815	5.36
	L PreC gyrus / Sup. frontal gyrus	-26	-9	55	4545	5.11
	L Middle temporal gyrus	-54	-62	2	1544	5.72
	L Superior parietal lobule	-9	-58	62	772	3.99
	L Inferior parietal lobule	-51	-34	44	1072	4.6
	R Inferior parietal lobule	40	-79	34	557	4
	L Cerebellum VII	-9	-72	-43	515	4.29
Control > PI	L SMA	-9	8	62	557	4.69
PD > PI	None					
PI > PD	L Cerebellum VII	-5	-76	-36	815	4.23

Table 4

ASL and English conjunction analysis for perspective-dependent and perspective-independent sentences. The clusters of activation from each map used in conjunctions were thresholded at $p < .05$, corrected.

Conjunction	Brain region	MNI coordinates			Voxels
		X	Y	Z	
<i>Perspective-Dependent</i>					
	R Superior frontal gyrus	24	-5	62	1200
	L Superior frontal gyrus	-24	-6	60	2872
	L Superior parietal lobule	-14	-61	56	686
	R Superior parietal lobule	18	-62	55	686
<i>Perspective-Independent</i>					
	R Superior frontal gyrus	24	-3	60	214
	L Superior frontal gyrus	-24	-4	58	2100
	L Supramarginal gyrus	-52	-31	44	986
	L Superior parietal lobule	-14	-58	60	557
	L Middle temporal gyrus	-54	-62	1	1329
	R Middle occipital gyrus	41	-77	31	557

Table 5

Group contrasts for Perspective-Dependent (PD) vs. control sentences, Perspective-Independent (PI) vs. control sentences. All contrasts were thresholded at $p < .05$, corrected. Submaximal peaks are listed in italics.

Contrast	Brain region	MNI coordinates			Voxels	Z score
		X	Y	Z		
PD ASL > English	L Inferior frontal gyrus	-33	29	-1	1801	5.27
	R Inferior frontal gyrus	54	12	27	3216	6.52
	R Caudate nucleus	9	12	9	986	4.16
	L Precentral gyrus	-51	8	34	858	3.89
	L Caudate nucleus	-5	5	9	1672	4.28
	L Middle frontal gyrus	-33	1	55	7975	6.98
	R Middle frontal gyrus	33	-1	58	6517	6.27
	L Cerebellum	-40	-48	-50	600	3.89
	L Superior parietal lobe	-16	-62	58	12,863	7.07
	<i>L Post central gyrus</i>	-33	-37	40		4.97
	L Middle occipital gyrus	-44	-79	-1	12,091	6.03
	<i>L Mid. occipital gyrus</i>	-33	-82	16		4.70
	R Superior parietal lobe	33	-77	40	30,999	6.55
	<i>R Sup. parietal lobe</i>	33	-44	58		6.59
	<i>R Post central gyrus</i>	33	-37	47		5.28
English > ASL	None					
PI ASL > English	R Middle frontal gyrus	40	5	55	900	4.03
	L Inferior parietal lobe	-30	-37	41	686	3.9
	R Superior parietal lobe	30	-44	54	3558	5.14
	R Middle temporal gyrus	50	-58	9	2015	4.66
	L Superior parietal lobe	-19	-62	58	1757	5.54
	R Middle occipital gyrus	33	-65	30	2443	4.53
	L Inferior occipital gyrus	-44	-79	-6	5273	5.17
English > ASL	L perirhinal cortex	-33	-2	-26	728	4.16
	L Insula	-37	-6	2	943	4.12
	R Insula	37	-16	9	814	3.86
	L Insula	-33	-20	9	1243	3.96