

# Neural Correlates of British Sign Language Comprehension: Spatial Processing Demands of Topographic Language

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## Abstract

■ In all signed languages used by deaf people, signs are executed in “sign space” in front of the body. Some signed sentences use this space to map detailed “real-world” spatial relationships directly. Such sentences can be considered to exploit sign space “topographically.” Using functional magnetic resonance imaging, we explored the extent to which increasing the topographic processing demands of signed sentences was reflected in the differential recruitment of brain regions in deaf and hearing native signers of the British Sign Language. When BSL signers performed a sentence anomaly judgement task, the occipito-temporal junction was activated bilaterally to a greater extent for topographic than nontopographic processing. The differential role of movement in the

processing of the two sentence types may account for this finding. In addition, enhanced activation was observed in the left inferior and superior parietal lobules during processing of topographic BSL sentences. We argue that the left parietal lobe is specifically involved in processing the precise configuration and location of hands in space to represent objects, agents, and actions. Importantly, no differences in these regions were observed when hearing people heard and saw English translations of these sentences. Despite the high degree of similarity in the neural systems underlying signed and spoken languages, exploring the linguistic features which are unique to each of these broadens our understanding of the systems involved in language comprehension. ■

## INTRODUCTION

At least two types of code structure can be identified for high-level representations of events and ideas in humans: a conceptual structure, coding linguistic representations; and an image structure, coding spatial representations (Jackendoff, 1996; Paivio, 1971). Spoken languages do not encode spatial distinctions directly, but have developed a range of lexical and pragmatic devices for doing so (see de Vega, Cocude, Denis, Rodrigo, & Zimmer, 2001; Kemmerer, 1999). By contrast, in signed languages, space can be used directly for linguistic expression (Sutton-Spence & Woll, 1999; Emmorey & Reilly, 1995; Engberg-Pedersen, 1993; Padden, 1988).

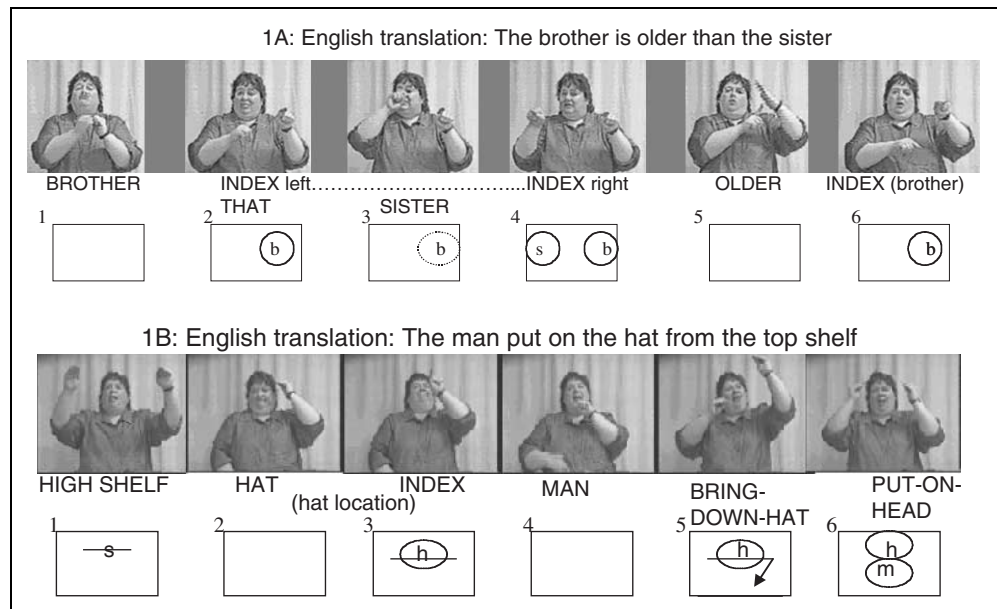
While the syntax of spoken language is primarily organized in a linear fashion, reflecting the temporal organization of the speech articulators and of hearing, syntax in signed languages exploits visuospatial organization. All signing occurs in the “sign space,” an area in front of the signer extending from the hips to just above the head, and the width of the extended elbows.

The use of sign space may be regarded as a continuum. At one extreme, sign space can be employed simply as a region for execution of signs in which the movement or location of signs is purely phonological (e.g., the British Sign Language [BSL] translation of “I like ice cream”). Further along this continuum, entirely abstract entities can be represented as spatially related. In the BSL translation of the sentence “Knowledge influences belief,” one location in the space in front of the signer is assigned to “knowledge,” a second location to “belief,” and the verb “influence” moves from the location of “knowledge” to that of “belief.” A similar use of space can be applied to more concrete sentences. For example, the English sentence “The brother is older than the sister” can be signed in BSL as shown in Figure 1A.

Such sentences are regarded as exemplifying “referential” use of space, in which spatial relations are used to differentiate grammatical classes and semantic roles. Space can also be used metaphorically in translations of sentences such as “The professor criticised the students,” where a higher location may be assigned to the higher status role of “professor,” with the verb moving downwards towards “students.” However, the

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**Figure 1.** Examples of nontopographic and topographic BSL sentences. Shown are the English translation of the BSL sentence, video images, and BSL glosses of the signed sentence and a schematic representation of the location of referents in sign space. 1A: Illustration of nontopographic BSL sentence. Frame 1—lexical sign for BROTHER (b). Frame 2—referential location for BROTHER established by indexing to the left. Frame 3—lexical sign for SISTER (s) is signed while the left hand maintains the location of BROTHER. Frame 4—referential location of SISTER is established using right hand. Frame 5—lexical sign for OLDER. Frame 6—referential location for BROTHER is indicated using left hand while the right hand returns to the rest position. BROTHER and SISTER use conventional locations: reference is achieved without regard to “actual” spatial relations. 1B: Illustration of topographic BSL sentence. Frame 1—the sign for SHELF is signed at a high location within sign space indicating the height of the target shelf. Frame 2—lexical sign for HAT. Frame 3—precise location of the hat on the shelf is indexed. Frame 4—lexical sign for MAN. Frame 5—the handling classifier handshape for HAT (holding a hat brim) is used to represent “bringing-down” the hat from the shelf located in Frame 1. Frame 6—HAT classifier used to indicate putting hat on MAN’s head.



locations of these events in sign space do not represent and are not constrained by “real-life” spatial relations. As concepts move to more concrete meanings, the extent to which real-world spatial features are represented can increase. Thus, at the far end of the continuum, signed languages can convey spatial relations directly: Sentences can be constructed “topographically.”

... In this case, the space within which signs are articulated is used to describe the position and orientation of objects or people. The spatial relations among signs correspond in a topographic manner to actual relations among objects described. The linguistic conventions used in this spatial mapping specify the position of objects in a highly geometric and nonarbitrary fashion by situating certain sign forms (e.g., classifiers) in space such that they maintain the topographic relations of the world-space being described. (Emmorey, Corina, & Bellugi, 1995, pp. 43/44)

An example of a BSL sentence at the topographic end of the continuum is shown in Figure 1B. Signed language grammar requires that the handshapes in verbs of motion and location in topographic sentences agree with real object features or classes (how objects are handled, their size and shape, or their function): These are signed language “classifiers” (Emmorey, 2001; Engberg-Pedersen, 1993; Supalla, 1986). In producing the verb in the current example, the handshape used denotes the handling of a flat object (the hat brim); the orientation of the hand captures the orien-

tion of the hat on the shelf, and the movement path of the verb echoes that taken when the hat is moved from the shelf to the head. All these features are simultaneously specified by the grammar and are characterized by features of the referent, orientation, and trajectory of action. For the purposes of this article, we will refer to sentence structures at this end of the continuum as “topographic” and all others as “nontopographic.”

Signed languages thus appear to differ from spoken languages, not only because space is obligatorily recruited for language, but additionally in that certain linguistic structures use spatial characteristics of semantic roles (classifiers) and spatial locations topographically. Such sentences map a number of spatial and image characteristics, both globally in terms of the relative locations of referents and the action paths that link them, and at a relatively fine grain, capturing local relationships (see Sutton-Spence & Woll, 1999).

At least one study in American Sign Language (ASL) suggests that this continuum between topographic and nontopographic sign representations has psychological reality. Emmorey et al. (1995) showed fluent ASL signers signed sentences followed by a probe item which could appear at a locus in the sign space that was congruent with the noun phrase in the test sentence or at an incongruent locus. Viewers made a speeded response indicating whether or not they had seen the probe before. Probes that had been indexed incorrectly were slower to process and more error prone, but the effect of probe incongruity was much greater for topographic than for nontopographic material. This study suggests

that spatial information is processed and represented differently when space serves a topographic function than when it does not. This raises the question addressed in the present report: Is there differential recruitment of cortical areas during topographic and nontopographic signed sentence comprehension?

A wide range of spatial functions have been associated with parietal lobe function in the hearing (for review, see Culham & Kanwisher, 2001). Thus, one might anticipate the parietal lobes to be involved in language comprehension tasks that demand spatial representational resources. However, this does not appear to be the case for spoken language. Although parietal regions may be activated in tasks such as solving spatial syllogisms when presented with a visual image (Carpenter, Just, Keller, Eddy, & Thulborn, 1999) or generation of spatial prepositions to visual images (Damasio et al., 2001), this does not appear to be mandatory (Reichle, Carpenter, & Just, 2000; Goel, Gold, Kapur, & Houle, 1998).

A different possibility is that the normal lateralization pattern for spoken language processing might be skewed for spatially demanding language tasks. There are at least two versions of the hypothesis that the right hemisphere may be involved in spatial language processing. The first is that the coordinate mappings of spatial relations are more efficiently assessed and assembled in the right than in the left hemisphere (Kosslyn et al., 1989). Second, the right hemisphere may be more adept at coordination and alignment of different spatial frameworks—viewer-centered, object-centered, and scene-centered (e.g., Bartolomeo & Chokron, 1999). However, this suggestion has not received much support from studies of spoken language. Patients with left hemisphere damage have impaired comprehension of spatial prepositions (such as “in,” “on,” “above”), whereas right hemisphere patients are impaired in processing relative location in spatial images (Kemmerer & Tranel, 2000). This suggests that even when space is referred to in spoken language, systems specialized for spatial processing are not specifically activated. Before considering whether the same is true of signed languages, the general cortical activation pattern for sign language processing will be summarized.

In general, cortical organization for signed language in native users is similar to that for spoken language (see Rönnerberg, Söderfeldt, & Risberg, 2000, for review). In a separate report (MacSweeney et al., 2002), BSL sentence comprehension in native signers was shown to localize in a very similar way to English in hearing people when the speaker was both seen and heard (audiovisual). Although activation was observed in both right and left hemispheres for both languages, it was predominantly left lateralized. The left inferior prefrontal and superior temporal regions were specifically recruited in both groups. Differences in activation between BSL and spoken English were also observed. These were related to the different sensory processing

requirements of the two languages. BSL recruited the posterior, visual processing, regions bilaterally to a greater extent than audiovisual speech, while speech recruited the auditory cortex in the lateral temporal lobes bilaterally more than BSL. In addition, BSL generated greater activation in the left inferior parietal lobe than audiovisual English. The finding that the parietal lobes are involved in sign language sentence comprehension is not novel (e.g., Neville et al., 1997). However, it raises the possibility that this region may be recruited to a greater extent when the spatial processing demands of sign language are increased, for instance, during topographic sentence comprehension.

Although there have been no systematic studies of differential processing of topographic and nontopographic material other than Emmorey et al.'s (1995) behavioral probe study, relevant case studies have been reported. Emmorey and colleagues have reported a hearing native ASL signer, DN, with damage to the right mesial superior parietal lobe extending into the occipital regions (Emmorey et al., 1995; Emmorey, 1996; see also Poizner & Kegl, 1992; Loew, Kegl, & Poizner, 1997, who refer to DN using the pseudonym AS). DN was impaired in producing and comprehending simple ASL commands involving classifiers, for instance, “place the pen on the book.” No such impairment was evident when the task was delivered in English, since here the spatial relation is encoded using the preposition “on.” In contrast, she was unimpaired in her comprehension and generation of ASL sentences involving spatial verbs (e.g., COME-TO; BRING), which make less topographic use of space than representing locations of objects. Emmorey has reported another patient with right hemisphere damage who shows a similar pattern to DN (Emmorey, 2001). AR has extensive damage to the right temporal lobe extending into the parietal and occipital lobes. AR was impaired at matching the location of a linguistic classifier in sign space with the position of the referent object in a picture, but not in her comprehension of ASL spatial prepositions such as “on” and “in.” Signers with left hemisphere damage showed the reverse pattern; impaired comprehension of prepositions but not classifiers (Emmorey, 2001).

Given that classifier constructions are topographically constrained; that is, the location and orientation of the classifier must be analyzed correctly to successfully interpret the sentence, these case studies suggest that topographically organized signed sentences may require right parietal processing. However, behavioral data from Emmorey and Corina (see Emmorey, 2001) suggest that the left parietal lobe may also play a role. They required signers to tap with their left or right hand as quickly as possible while watching signed topographic and nontopographic sentences. The greatest decrement was seen in right-hand tapping while watching both sentence types. The decrement was interpreted as indicating the predominant involvement

of the left hemisphere in processing both topographic and nontopographic sentences.

### Experimental Strategy

On the basis of lesion studies and behavioral work with hearing participants, we predict that the parietal lobes will be recruited to a greater extent by topographic sentence processing than nontopographic, however, the laterality of the predicted differential activation is unclear. To test this, native BSL signers performed a sentence anomaly judgement task and low level baseline task in the MR scanner. In one experimental condition, the signed sentences were topographic, in the other, they were nontopographic (see Methods for details and Appendix for English translations of sentences). Congenitally deaf and hearing native signers were scanned. All had learned BSL from their deaf parents.

We also investigated whether audiovisual spoken English translations of the BSL sentences generated task-specific differences in activation. If the topographic/nontopographic distinction was confounded with the extent to which the sentences required “post-linguistic” spatial analysis, mapping from a linguistic to a conceptual level, this contrast should show a similar pattern in spoken English as in BSL.

## RESULTS

### BSL Comprehension

#### Behavioral Data

One hearing signer misunderstood the instructions. Those data are excluded from all the analyses reported here. For the remaining participants, errors were categorized either as “misses,” where the anomalous sentence was not detected at all, or erroneous identification of the target. Deaf subjects performed with 91% accuracy in both the topographic and nontopographic conditions. Hearing native signers were less accurate; 75% topographic, 85% nontopographic (see Table 1). The discrepancy in performance between

**Table 1.** Accuracy on Anomalous Sentence Task as a Function of Sentence Type

Group	Sentence Type	Mean % Accuracy (SD)
Deaf signers— BSL stimuli ( $n = 9$ )	Topographic	91.1 (14.5)
	Nontopographic	91.1 (10.5)
Hearing signers— BSL stimuli ( $n = 8$ )	Topographic	75 (20.7)
	Nontopographic	85 (14.1)
Hearing—English stimuli ( $n = 8$ )	Topographic	90 (15.1)
	Nontopographic	97.5 (7.1)

deaf and hearing native signers was accounted for in the fMRI analyses by splitting the hearing group into high and low accuracy subgroups.

#### fMRI Data

Contrasts between topographic and nontopographic conditions, relative to baseline, are reported (see Methods and Tables 2 and 3).

#### Topographic Compared with Nontopographic Sentences

*Deaf signers.* Deaf signers generated greater activation during topographic than nontopographic sentence comprehension (see Tables 2 and 3 and Figure 2). Greater topographic-related activation was observed bilaterally at the occipito-temporal junction, incorporating posterior parts of the middle temporal gyrus, and bilaterally in the inferior frontal gyrus. Greater activation was also generated in response to topographic sentences in the left inferior parietal lobule (IPL; BA 40) and in the left superior parietal lobule (SPL), in the upper bank of the parieto-occipital sulcus (BA 7).

*Hearing signers.* As observed in the deaf group, hearing signers generated greater topographic-related activation in the posterior middle temporal gyri bilaterally and in the left IPL. Bilateral frontal activation was also observed, however, this was more inferior to that seen in the deaf group. The differential parietal activation was less extensive than in the deaf group. Task performance by hearing signers was more variable than in the deaf signers, suggesting that task accuracy, rather than hearing status, may underlie this “diluted” parietal activation. The group was therefore split into two subgroups. The low accuracy group included those who made two or three errors on either sentence type out of a possible total of five ( $n = 4$ ), the high accuracy group made one or no errors ( $n = 4$ ). Enhanced left parietal activation for topographic relative to nontopographic sentences was observed in the high accuracy subgroup only. This involved two regions: the left IPL (BA 40;  $x = -40$  mm,  $y = -59$  mm,  $z = 42$  mm; number of voxels = 4; voxel size =  $3 \times 3 \times 5.5$  mm) and the SPL (BA 7;  $x = -32$  mm,  $y = -63$  mm,  $z = 48$  mm; number of voxels = 12).

#### Nontopographic Compared with Topographic Sentences

*Deaf signers.* Deaf signers generated extensive bilateral activation in the inferior frontal gyrus in response to nontopographic relative to topographic sentences. This activation was anterior and inferior to the frontal activation observed for topographic sentences (see Table 3). They also generated enhanced bilateral putamen, left superior temporal gyrus, and right cerebellum activation.

**Table 2.** Brain Regions Activated More by Topographic Sentences than Nontopographic Sentences, Relative to Baseline Condition

<i>Cerebral Region (Brodmann's Area)</i>	<i>No. of Voxels</i>	<i>Coordinates (mm)</i>		
		<i>x</i>	<i>y</i>	<i>z</i>
<i>Deaf (BSL)</i>				
L. Posterior middle temporal gyrus (21/37)	88	-42	-61	3
R. Posterior middle temporal gyrus (21)	65	48	-51	1
R. Inferior frontal gyrus (44)	29	47	13	27
L. Inferior parietal lobule (40)	17	-55	-37	32
L. Superior parietal lobule/parieto-occipital sulcus (7)	12	-17	-76	34
R. Posterior middle temporal gyrus (39)	9	45	-64	17
L. Inferior frontal gyrus (44)	8	-48	6	32
R. Cerebellum	7	44	-51	-21
L. Inferior parietal lobe (40)	6	-56	-32	22
<i>Hearing (BSL)</i>				
R. Posterior middle temporal gyrus (21)	92	46	-56	1
L. Posterior middle temporal gyrus (21)	49	-49	-49	7
R. Middle frontal gyrus (47)	32	39	47	-6
R. Middle frontal gyrus (47)	25	23	44	-9
L. Middle frontal gyrus (9)	16	-36	3	40
L. Occipital gyrus (18/19)	9	-24	-79	23
R. Medial geniculate body	5	17	-24	-2
L. Orbito-frontal cortex (11)	5	-32	45	-18
L. Inferior parietal lobule (40)	5	-34	-51	42
<i>Control experiment: Hearing nonsigners (audiovisual English)</i>				
L. Anterior middle temporal gyrus (21)	16	-50	-13	-4
R. Superior frontal gyrus (10)	6	30	56	-4
R. Cerebellar vermis	5	4	-47	4
R. Posterior inferior temporal gyrus (37)	5	49	-56	-7
R. Superior temporal gyrus (22)	5	57	-7	4

Coordinates represent centroids of 3-D clusters ( $p < .00125$ ).

*Hearing signers.* Hearing signers also showed greater activation in the right putamen, the left superior temporal gyrus, and the right cerebellum during nontopographic than topographic sentence comprehension. Additional regions of differential activation are listed in Table 3.

### **Control Experiment—Audiovisual English Sentences**

Mean accuracy of the hearing nonsigners performing the anomalous sentence identification task in English

was high; topographic 90%; nontopographic 97%. As Tables 2 and 3 show, audiovisual English sentences presented to hearing nonsigners did not generate contrastive activation patterns resembling that for BSL sentences. Activation was greater for the nontopographic than topographic sentences and these differences were smaller in extent than in signers. The primary finding was a difference in laterality of processing of sentence types within the anterior middle temporal gyrus; topographic—left; nontopographic—right. Further experiments are necessary to explore the functional relevance of this distinction. Importantly, no

differential parietal activation was observed between sentence types.

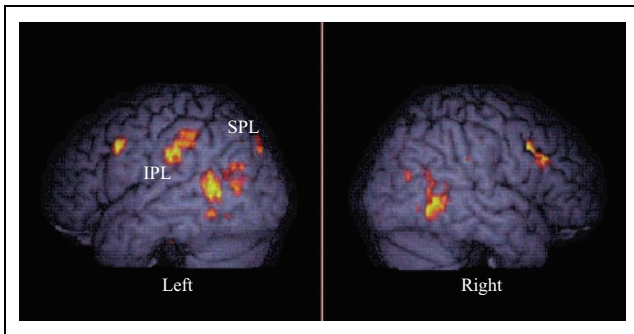
To test our hypothesis that enhanced parietal activation would be specific to BSL, we focused on the largest cluster of parietal activation in the deaf group (centroid  $x = -54$  mm,  $y = -37$  mm,  $z = 37$  mm; voxels = 6; this

is a 2-D cluster of voxels which is part of the largest IPL 3-D cluster listed in Table 2). The difference in power of response in this region between topographic and nontopographic conditions (relative to baseline) was established for each deaf signer and each hearing participant in the spoken English experiment. Differential activation

**Table 3.** Brain Regions Activated More by Nontopographic Sentences than Topographic Sentences, Relative to Baseline Condition

<i>Cerebral region (Brodmann's Area)</i>	<i>No. of Voxels</i>	<i>Coordinates (mm)</i>		
		<i>x</i>	<i>y</i>	<i>z</i>
<i>Deaf (BSL)</i>				
R. Inferior frontal gyrus (45)	27	48	25	10
L. Putamen	20	-16	8	3
L. Superior temporal gyrus (22)	16	-51	-34	8
L. Inferior frontal gyrus (45)	12	-40	27	11
R. Inferior frontal gyrus (46)	10	40	41	7
R. Putamen	10	17	15	2
R. Middle frontal gyrus (46/9)	9	34	35	26
R. Inferior temporal gyrus (20)	9	45	-19	-13
R. Cerebellum	5	24	-78	-24
<i>Hearing (BSL)</i>				
L. Lingual gyrus (18)	21	-15	-84	-4
L. Inferior frontal gyrus (44)	20	-48	10	15
R. Middle temporal gyrus (21)	15	51	-21	-7
L. Posterior cingulate (31)	14	-26	-27	40
L. Inferior temporal gyrus (19)	11	-41	-66	-2
R. Fusiform gyrus (18/19)	9	26	-84	-10
R. Cerebellum	7	28	-58	-24
L. Fusiform gyrus (37)	6	-43	-46	-13
L. Superior temporal gyrus (22)	6	-44	-52	20
R. Putamen	5	9	7	4
R. Cerebellum	5	28	-76	-24
L. Middle temporal gyrus (39)	5	-32	-67	20
<i>Control experiment: Hearing nonsigners (audiovisual English)</i>				
R. Anterior middle temporal gyrus (21)	58	56	-18	-8
L. Superior temporal gyrus (22)	17	-51	-48	15
R. Superior temporal gyrus (22)	7	43	-22	15
L. Lateral sulcus	6	-52	-33	20
L. Anterior cingulate (32)	6	-13	33	23
R. Superior/medial frontal gyrus (11)	6	13	40	42

Coordinates represent centroids of 3-D clusters ( $p < .00125$ ).



**Figure 2.** Locations of peak activation during topographic relative to nontopographic sentence processing in deaf native signers of BSL. Activation up to 5 mm beneath the surface of the cortex is displayed. For a more comprehensive description of the data, see Table 2. IPL = inferior parietal lobule (BA 40); SPL = superior parietal lobule (BA 7).

was significantly greater in the deaf signers than in the hearing English speakers [ $t = 2.93$  (15),  $p < .02$ ].

## DISCUSSION

Comprehension of topographic BSL sentences recruited the left parietal and bilateral posterior middle temporal cortices to a greater extent than nontopographic sentences. Importantly, activation in these regions was specific to BSL and was not observed in hearing people watching audiovisual English translations of the sentences. Thus, it is unlikely that mapping from the linguistic to conceptual level (i.e., postlinguistic factors) differed in the two sentence types.

Our experimental predictions were open concerning the lateralization of the hypothesized differential parietal activation. We observed enhanced activation at two sites within the left parietal lobe. The most extensive of these was localized within the IPL (BA 40) and was superior to the region often activated in text reading studies (e.g., Horwitz, Rumsey, & Donohue, 1998). The second area of activation was in the SPL (BA 7), in the deaf signers this was located in the upper bank of the parieto-occipital sulcus. The finding that the left parietal lobe should be recruited to a greater extent than the right is supported by Emmorey and Corina's (see Emmorey, 2001) tapping study reviewed in the Introduction. However, this pattern appears to conflict with Kosslyn's conceptualization of "categorical" left hemisphere and "coordinate" right hemisphere organization for spatial representations (Kosslyn et al., 1989). Topographic sentences require "coordinate" mappings of the position of each hand. Rather the data appear to fit better with the more general idea that the left hemisphere is associated with a local rather than a global processing style (Hellige, 1993). However, both these general models may be less applicable to the present results than more specific findings regarding processing of manual gestures and actions.

Gerardin et al. (2000) have shown that the left IPL is involved in imagery of hand movements when contrasted with actual movement. Their reported foci of activation ( $x = -48$  mm,  $y = -36$  mm,  $z = 42$  mm) is similar to those reported here in relation to topographic BSL sentences (hearing:  $x = -34$  mm,  $y = -51$  mm,  $z = 42$  mm; deaf:  $x = -55$  mm,  $y = -37$  mm,  $z = 32$  mm extending superiorly). Kosslyn, DiGirolamo, Thompson, and Alpert (1998) also report this region to be activated during imagery of hand rotation ( $x = -50$  mm,  $y = -32$  mm,  $z = 40$  mm). A recent PET study of recognition of "meaningless" hand gestures, using still images, reports a specific role for the left IPL in hand position discrimination (Hermsdörfer et al., 2001). The foci for the relevant experimental contrast ( $x = -54$  mm,  $y = -40$  mm,  $z = 46$  mm) were, again, similar to those reported here within the left IPL. Thus, we argue that the additional processing in this region during comprehension of topographic signed sentences reflects the necessary precise coordinate mapping of hand-shapes, locations, and movements. This hypothesis is supported by the finding that only hearing native signers who performed the task well showed differential left IPL activation. One contributor to the slightly poorer behavioral performance by hearing native signers may be that deaf parents may interact with their deaf and hearing children differently, which is likely to influence sign language skill (van de Bogaerde, 2000).

An integral part of topographic signed utterances are classifiers, the meaning of which are interpreted on the basis of their handshape and location. This raises the question of how to reconcile our finding of left hemisphere recruitment for topographic sentences with case DN (Emmorey et al., 1995). DN is an ASL signer with right hemisphere damage, who was impaired in matching a signed classifier to a pictured object. She was also impaired in the production of a signed spatial description of the items in a room. It is plausible that the requirement in these tasks to coordinate different spatial frameworks, one given by the picture or real scene and one in a topographic linguistic structure, demands skills dependent upon the right parietal regions. This was not required in the sentence acceptability task in the present study. Our suggestion, then, is that simple comprehension of topographic sentences may require left parietal regions to a greater extent than right. However, mapping the linguistic information to or from another framework, such as a visual scene, may recruit the functions of the right hemisphere (see Emmorey et al., 2001). The increased demands of discourse, where referents' locations need to be maintained across several sentences, may also place greater demands on right hemisphere processing resources.

A second area within the left parietal lobule to be recruited more for topographic than nontopographic sentence processing was the SPL (BA 7). In the deaf subjects, this was localized in the upper bank of the

parieto-occipital sulcus. A similar account for the enhanced involvement of this area in topographic sentence processing may be proposed as for the inferior parietal activation, since this area is also known to be involved in monitoring finger movement (e.g., Weeks, Honda, Catalan, & Hallett, 2001). An alternative explanation relates to action processing. The SPL is thought to be involved in the execution, simulation, and observation of action (see Grèzes & Decety, 2001). Using PET, Damasio et al. (2001) reported activation in the left parieto-occipital sulcus when hearing participants generated action terms from still images in contrast to control conditions of object naming or a face orientation task. Naming of actions, whether with tools (e.g., “stirring”;  $x = -21$  mm,  $y = -82$  mm,  $z = 32$  mm) or without tools (e.g., “running”;  $x = -20$  mm,  $y = -81$  mm,  $z = 34$  mm), generated activation close to that reported here ( $x = -17$  mm,  $y = -76$  mm,  $z = 34$  mm). Although content of sentences used in our experiment was matched as far as possible, the topographic sentences included slightly more action terms than nontopographic sentences. Note that in the current study enhanced SPL activation was not observed in hearing nonsigners listening to the topographic and nontopographic sentences in English. Therefore, SPL activation in the deaf group cannot simply be due to semantic differences between the sentences. Rather, one possibility is that seeing the BSL signs for action terms is more akin in processing requirements to seeing an image of an action, as in the Damasio et al. study, than when hearing the action term spoken in English. This plausibility of this possibility requires further research.

### **Enhanced MT Activation for Topographic Sentences**

Topographic signed sentences generated greater activation at the occipito-temporal junction bilaterally than nontopographic sentences. This activation included regions specialized for the processing of real-world visual movement (V5a/V5/MT: e.g., Kourtzi & Kanwisher, 2000; Senior et al., 2000). Three hearing non-signers tested on the two types of BSL sentences did not show differential activation of MT. Therefore, the movement content of the sentences is unlikely to differ.<sup>1</sup> Rather, it is possible that this activation reflects top-down modulation of MT.<sup>2</sup> Such top-down modulation of activation within MT has been shown in studies manipulating attention (Rees, Frith, & Lavie, 1997) and in presentation of stilled images in which motion is implied, such as a falling cup (Senior et al., 2000). Movement within many of the topographic sentences in this study specified either the location or movement of a referent, for example, a hat being brought down from a shelf. Whereas, in most of the nontopographic sentences, the movement of the verb was phonological and did not refer to the movement or location of the referent. Thus, move-

ment must be interpreted differently according to sentence type, perhaps accounting for the differential middle temporal activation.

### **Conclusion**

In signed languages, it is possible to distinguish sentences, which use spatial descriptors to map natural spatial relations, and sentences where spatial location, while used contrastively, is not specified to the same degree. We have reported brain activation patterns specific to this linguistic contrast in BSL. Relative to nontopographic sentence processing, topographic sentences recruited bilateral occipito-temporal regions and left inferior and superior parietal regions. We propose that signed languages may recruit visual movement processing cortices differentially depending on whether movement of signs is purely phonological or whether it reflects movement or location of a referent. Second, we propose that the recruitment of the left IPL facilitates the discrimination and representation of signs necessary for the successful comprehension of signed sentences, which directly map spatial relationships. In topographic sentences, the image structure and the conceptual structure (Jackendoff, 1996) are coincident. This feature, unique to signed languages, may account for the differential cortical recruitment observed during comprehension of signed spatial concepts.

### **METHODS**

#### **Stimuli**

Stimuli were topographic and nontopographic BSL sentences matched for duration and concreteness (see Appendix for English translations and [www.ich.ucl.ac.uk/macsweney/jocnstimuli/](http://www.ich.ucl.ac.uk/macsweney/jocnstimuli/) for BSL glosses). The topographic sentences contained an average of 2.37 nouns (range 1–3); the nontopographic sentences, 2.21 nouns (range 1–3). None of the nontopographic sentences included classifiers; there was an average of 1.08 classifiers per sentence in the topographic sentences (range 0–2). The sentence sets also included 10 semantically anomalous but grammatical sentences. One appeared in each block as the target sentence. Five were topographic (e.g., The carpet is under the house) and five were nontopographic (e.g., The computer screen is worried). Correct and anomalous sentences could not be distinguished “by eye.” That is, the anomalous sentences maintained correct spatial relationships and classifiers. For instance, in “The carpet is under the house,” the appropriate classifier for “flat object” (CARPET) was located by the signer below the sign for HOUSE.

#### **Participants**

Eighteen right-handed signing participants were tested. All were native signers and had learned BSL from their

deaf parents. Nine were congenitally profoundly deaf (5 men, 4 women). Their mean age was 30 years 5 months (range 18–48 years). All deaf participants performed at or above an age-appropriate level on a test of nonverbal IQ (Block Design, WAIS-R). Nine hearing native signers were also tested (3 men, 6 women). Their mean age was 32 years 8 months (range 20–51 years). There was no significant difference between the groups on a test of BSL [ $t = 1.12 (14), p > .1$ ]. This was a development of Herman, Holme, and Woll (1999) test of BSL comprehension in children. The BSL stimuli were refilmed to ensure the sign style was more suitable for deaf adults and lip-reading cues were omitted. All participants were right-handed and without known neurological or behavioral abnormality. The groups were closely matched on educational achievement. Four deaf native signers and four hearing native signers had completed tertiary education. All gave written informed consent to participate in the study, which was approved by the relevant Research Ethics Committees.

### **Experimental Design**

Subjects watched alternating blocks of topographic and nontopographic BSL sentences interspersed with a baseline task. These were produced by a native deaf signer and presented on a video display. Five blocks of topographic sentences and five blocks of nontopographic sentences were presented in this way, with 10 blocks of the baseline task. All blocks lasted 21 sec and included five sentences or baseline events. The total run lasted 7 min. The experiment started with a baseline block. The order of presentation of the topographic/nontopographic blocks was then counterbalanced across participants.

#### *Experimental Conditions—Topographic/ Nontopographic Sentence Comprehension*

In each 21-sec block, participants watched five topographic or nontopographic BSL sentences. They were told that one of the sentences in each block did not make sense (e.g., The bicycle kicked the pig). Their task was to identify the semantically anomalous sentence using the button box held in their right hand.

#### *Baseline Condition*

This required the participant to view the signer at rest, while monitoring the display for a change (a vigilance task). A small dark square was digitally superimposed on the signer's chin. It appeared five times for 1000 msec in each block. In four presentations, the cue was black, but in one presentation, it was gray. Participants were required to make a button press response to the gray cue. The baseline task thus controlled for the attentional and motor-response param-

eters of the experimental task, and for the perception of a face and body. All participants practiced the experimental and baseline tasks outside the scanner. In both the experimental and baseline blocks, the target sentence or target cue was presented pseudo-randomly in the third, fourth, or fifth position to maintain attention throughout the block. The videotaped stimuli were projected onto a screen located at the base of the scanner table via a Proxima 8300 LCD projector. The stimuli were projected to a mirror angled above the subject's head in the scanner.

### **Control Experiment: Audiovisual English Translations**

Eight hearing nonsigners were also scanned (4 men, 4 women; mean age 26:3 years; range 18–40 years). This experiment was similar in design to the experiment outlined above, however, the experimental blocks were made up of English translations of the BSL topographic and nontopographic sentences. These were spoken by a native English speaker and presented audiovisually with similar image characteristics to the sign display (i.e., upper torso; plain background). In the baseline task, the participants watched a still image of the speaker and were required to attend to an auditory, rather than visual, cue. Four short 500-Hz tones and one 1500-Hz tone were presented in each 21-sec block. The participant was required to make a button press response to the high tone. The imaging and analysis parameters were the same as outlined below for the BSL experiment.

### **Imaging Parameters**

Gradient-echo echo-planar MRI data were acquired with a 1.5-T General Electric MR system fitted with Advanced NMR hardware and software using a standard quadrature head coil. Head movement was minimized by positioning the subject's head between cushioned supports. One hundred-forty  $T_2^*$ -weighted images depicting BOLD contrast were acquired with a slice thickness of 7 mm (with 0.7 mm interslice gap). Fourteen axial slices were acquired in each volume to cover the whole brain (TR = 3 sec, TE = 40 msec). An inversion recovery EPI dataset was also acquired to facilitate registration of each individual's fMRI dataset to Talairach space (Talairach & Tournoux, 1988). This comprised of 43 near-axial 3 mm slices (0.3 mm gap), which were acquired parallel to the AC–PC line (TE = 80 msec, TI = 180 msec, TR = 16 sec).

### **Data Analysis**

#### *Group Analysis*

Following motion correction, a least-squares fit was carried out between the observed time series at each voxel and a mixture of two one-parameter gamma

variate functions (peak responses 4 and 8 sec) convolved with the experimental design (Friston, Josephs, Rees, & Turner, 1998). A statistic describing the standardized power of response was derived by calculating the ratio between the sum of squares due to the model fit and the residual sum of squares (SSQ ratio). Significant values of this statistic were identified by comparison with its null distribution computed by repeating the fitting procedure ten times at each voxel after wavelet-based permutation of the time series (Bullmore et al., 2001). This procedure preserves the noise structure of the time series during the permutation process and gives good control of Type I error rates. The voxel-wise SSQ ratios calculated for each subject from the observed data and following time series permutation were transformed into the standard space of Talairach and Tournoux (1988) as described previously (Brammer et al., 1997). Median activation maps (voxel-wise probability of false activation of  $<.00004$ ) were computed separately for each group after smoothing the statistic maps with a gaussian filter (FWHM 7.2 mm).

Areas showing differential activation to topographic and nontopographic sentences, relative to baseline, were identified using voxel-wise permutation tests. Significant voxels are shown superimposed on a structural MRI image in the stereotactic space of Talairach and Tournoux (1988, see Figure 2). Since the data were smoothed, it is possible that some Type 1 error voxels may form clusters. In order to avoid unwarranted interpretation of activations, which could be random Type 1 errors, only clusters of greater than four voxels are reported (Tables 2 and 3). Further details of the bootstrap experiment used to determine the appropriate voxel level for this type of experiment are reported in MacSweeney et al. (2001). The analysis of regions activated by “both” sentences types is reported in MacSweeney et al. (2002).

### *Secondary Analysis in Deaf Signers*

Correlational analyses were carried out to assess the relationship between left parietal and occipito-temporal regions activated significantly more by topographic than nontopographic sentences in deaf signers, since it could be argued that the parietal activation was “driven” by MT activation. Four 2-D clusters, which comprise the 3-D clusters listed in Table 2, were selected. These were the largest IPL cluster ( $x = -54$  mm,  $y = -37$  mm,  $z = 37$  mm; no. of voxels = 6), the largest SPL cluster ( $x = -14$  mm,  $y = -78$  mm,  $z = 37$  mm; no. of voxels = 6), and two regions within the occipito-temporal region. The first occipito-temporal area was selected on the basis that it fell within the motion cortex, as functionally defined in a study of motion perception performed on the same MR scanner as used in the current study (Senior et al., 2000;  $x = -47$  mm,  $y = -67$  mm,  $z = 15$  mm; 14 voxels). For completeness,

an area more likely to be considered “classical” V5 was also selected. The bases for the selection of this cluster were the mean coordinates (and standard deviations) reported by Hasnain, Fox, and Woldorff, (1998) in a meta-analysis of intersubject variability of visual areas—V5:  $x = -39$  mm (2.6),  $y = -71.9$  mm (4.2),  $z = -0.8$  mm (4.1). Although the centroid coordinates of our most appropriate cluster ( $x = -36$  mm,  $y = -78$  mm,  $z = 9$  mm; 23 voxels) fall slightly superior to this region, there was an overlap between the two.

The standardized power of response, relative to baseline (model sum of squares/residual sum of squares—see above under “Group analysis”) for the nontopographic sentences, was subtracted from that for topographic sentences for each individual in each of the four ROIs. This yielded, for each deaf subject, a measure of the difference in brain activation in each ROI, corrected for variations in noise level in each experiment. The product-moment correlation coefficient of these differences between each ROI was then calculated over all the deaf participants. This allowed us to compute to what extent the change in activation in one region might be dependent on the change in another region. As would be predicted, activation within the two visual regions was strongly correlated [ $r = .95$  (9);  $p < .0005$ ]. However, activation in neither of these regions correlated significantly with activation in IPL [(i)  $r = .56$  (9),  $p > .1$ ; (ii)  $r = .47$  (9),  $p > .1$ ] or SPL [(i)  $r = -.07$  (9),  $p > .1$ ; (ii)  $r = -.188$  (9),  $p > .1$ ]. Although null results should be interpreted with caution, given the small sample size, these findings suggest that parietal activation was not entirely determined by activation in visual processing areas.

## **APPENDIX 1: ENGLISH TRANSLATIONS OF BSL STIMULI**

### **Topographic Sentences**

The book is next to the pen on the table.  
 The woman handed the boy a cup.  
 Paddington is to the west of Kings Cross.  
 The man put on the hat from the top shelf.  
 The bicycle kicked the pig.<sup>a</sup>  
 I flew from London to Dublin.  
 The cat sat on the bed.  
 The videos were lined up on five shelves.  
 The cup climbed over the sheep.<sup>a</sup>  
 The bouncer punched the man in the face.  
 I parked the car next to the truck.  
 The woman shaved her legs.  
 On the plane the boy sat next to the window.  
 I drove to the conference from London.  
 The pen ran very fast.<sup>a</sup>  
 The girls hid under the table.  
 The boy hung his coat on the coatstand.  
 I planted the flowers between the tree and the bush.  
 The carpet is under the house.<sup>a</sup>  
 The three wrecked cars lay on top of each other.  
 They hid under the bridge when it rained.  
 The keys are hanging on the rack on the left.

The car turned left and ran into a lorry.  
The two women bumped into each other in the street.  
The book was full of cows.<sup>a</sup>

### Nontopographic sentences

The electricity bill was big but the gas bill was huge.  
I copied the design of the dress.  
My Aunt's necklace is my favourite.  
The kettle lectured the clock.<sup>a</sup>  
Coronation Street is much better than Eastenders.  
I will send you the date and time.  
This building is being renovated.  
The boy ran for hours and hours.  
Smoking is bad for your health.  
The computer screen is worried.<sup>a</sup>  
The old window was broken.  
We could have a camping, B&B or self catering holiday.  
Yesterday I interpreted for all of them.  
You can have an apple or an orange.  
My cupboard is depressed.<sup>a</sup>  
The boy laughed at the story.  
The child was upset when he fell.  
My friend didn't like the film.  
The brakes on the bicycle are pencils.<sup>a</sup>  
Asda is much cheaper than Waitrose.  
The man filmed the wedding.  
The man cut the cake into four pieces.  
Those two women are sisters.  
The brother is older than the sister.  
The teacher broke his tie.<sup>a</sup>

<sup>a</sup>Denotes target anomalous sentence.

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The data reported in this experiment have been deposited in The fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2002-112R1.

### Notes

1. A computational algorithm to determine the amount of movement in a series of ordered image frames (Johnston, McOwan, & Benton, 1999) also suggests the topographic and nontopographic stimuli did not differ in their movement content.
2. We are grateful to Karen Emmorey for highlighting this possible interpretation of the data.

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