

Sign and speech: amodal commonality in left hemisphere dominance for comprehension of sentences

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Summary

The neural basis of functional lateralization in language processing is a fundamental issue in systems neuroscience. We used functional MRI (fMRI) to examine hemispheric dominance during the processing of signed and spoken sentences. By using tasks involving comprehension of sentences (Sc) and sentential non-word detection (Sn), we compared different groups and stimulus conditions. Under the sign condition with sentence stimuli in Japanese Sign Language (JSL), we tested two groups of subjects: Deaf signers (Deaf) of JSL, and hearing bilinguals (children of Deaf adults, CODA) of JSL and Japanese (JPN). Under the speech condition, we tested hearing monolinguals (Mono) of JPN with auditory JPN stimuli alone (AUD), or with an audiovisual presentation of JPN and JSL stimuli (A&V). We found that the overall bilateral activation patterns under the four experimental conditions of Deaf, CODA, AUD and A&V were almost

identical, despite differences in stimuli (JSL and JPN) and groups (Deaf, CODA and Mono). Moreover, consistently left-dominant activations involving frontal and temporoparietal regions were observed across all four conditions. Furthermore, irrespective of the modalities of sign and speech, the main effects of task (Sc–Sn) were found primarily in the left regions: the ventral part of the inferior frontal gyrus (F3t/F3O), the precentral sulcus, the superior frontal gyrus, the middle temporal gyrus, the angular gyrus and the inferior parietal gyrus. Among these regions, only the left F3t/F3O showed no main effects of modality condition. These results demonstrate amodal commonality in the functional dominance of the left cortical regions for comprehension of sentences, as well as the essential and universal role of the left F3t/F3O in processing linguistic information from both signed and spoken sentences.

Keywords: deaf; sign language; speech; functional lateralization; frontal cortex

Abbreviations: AG = angular gyrus; ASL = American Sign Language; AUD = auditory JPN stimuli alone; A&V = audiovisual presentation of JPN and JSL stimuli; BA = Brodmann area; BSL = British Sign Language; CODA = hearing bilinguals, children of Deaf adults; Deaf = Deaf signers; F1 = superior frontal gyrus; F2 = middle frontal gyrus; F3O = inferior frontal gyrus, orbital part; F3t = inferior frontal gyrus, triangular part; fMRI = functional MRI; IPG = inferior parietal gyrus; JPN = Japanese; JSL = Japanese Sign Language; L1 = first language; L2 = second language; Mono = hearing monolinguals; MTG = middle temporal gyrus; PrCS = precentral sulcus; R = repetition detection; Sc = comprehension of sentences; SMG = supramarginal gyrus; Sn = sentential non-word detection; STG = superior temporal gyrus

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Introduction

There are still many unanswered questions about brain asymmetry and functional lateralization of the two hemispheres in both basic and clinical neurosciences (Geschwind and Galaburda, 1987; Hellige, 1993; Davidson and Hugdahl,

1995; Gazzaniga, 2000; Toga and Thompson, 2003). It is generally believed that language processing is mostly lateralized to the left hemisphere, as repeatedly reported by language studies using functional MRI (fMRI), PET and

other neuroimaging techniques. However, recent fMRI studies by Neville and colleagues showed that the processing of American Sign Language (ASL) recruited the bilateral cortical areas of both deaf native signers and hearing native signers of ASL, while the processing of written English was left lateralized (Neville *et al.*, 1998; Newman *et al.*, 2002). It should be noted that for the deaf signers, ASL was their first language (L1), and written English their second (L2). Another fMRI study reported bilateral cortical activation for the processing of British Sign Language (BSL), but without evidence of enhanced right hemisphere recruitments in sign language when compared with an audio-visual speech condition (MacSweeney *et al.*, 2002b). Moreover, PET studies have reported left-lateralized activation of the inferior frontal cortex during 'inner signing' of sentences or verb generation (McGuire *et al.*, 1997; Petitto *et al.*, 2000). It is thus a considerable challenge to clarify 'what's right and what's left' (Paulesu and Mehler, 1998; Hickok *et al.*, 1998). On the other hand, Bellugi and colleagues have established that sign language aphasia is due primarily to left-hemisphere lesions (Poizner *et al.*, 1987; Bellugi *et al.*, 1989). It has been pointed out that language production, upon which the assessment of aphasia has largely been determined, is highly lateralized, whereas sentence comprehension is bilaterally represented in the case of sign language (Corina *et al.*, 1998). Therefore, it remains to be clarified whether comprehension of sentences is functionally lateralized in either sign or speech.

One possible factor for right frontal activation is prosody, which marks syntactic boundaries and adds certain semantic or emotional information to sentences. It has been indicated that sign movements operate as the most basic prosodic units of the language (Brentari, 1999). Lesion studies have reported that patients with right frontoparietal damage spoke essentially in a monotone voice, without prosody (Ross and Mesulam, 1979), and a recent fMRI study has shown enhanced right frontal activation during an explicit task for evaluating the prosody of spoken sentences (Plante *et al.*, 2002). Another factor for the right hemispheric activations might be expressing or encoding spatial relations with signs (Hickok *et al.*, 1996), but, according to a recent PET study of expressing spatial relations in ASL, neither left nor right frontal regions showed positive activation (Emmorey *et al.*, 2002).

With regard to spoken language sentence comprehension, we recently reported that the left frontal regions are preferentially activated, a fact which cannot be explained by general cognitive factors such as task difficulty and short-term memory (Hashimoto and Sakai, 2002). If the basic neural mechanisms of sentence comprehension are universal between signed and spoken languages, left-lateralized activations should be consistently observed. To our knowledge, however, no previous research directly comparing sign language comprehension in deaf signers with auditory speech comprehension in hearing non-signers has been conducted. In this study, therefore, we targeted comprehension of sentences which requires processing of linguistic information not only

at the word and phrase levels, but at the sentence and discourse levels, so that highly structured and highly productive processes of language could be examined (Townsend and Bever, 2001). Using fMRI, we explored the extent to which sign language comprehension and speech comprehension activate similar brain regions, when the task is perceiving sparsely occurring anomalies in discourse compared with perceiving lexical anomalies. The present study was also designed to minimize emotional or other non-linguistic factors that might affect cortical activations. Video-taped images showing the full frontal profile of each signer were presented as signed stimuli, whereas synthesized speech sounds were used as spoken stimuli. These stimuli contained linguistic information that was necessary and sufficient to comprehend dialogue sentences. We have already established that synthesized speech stimuli elicit activations in bilateral early auditory areas and left-lateralized language areas (Hashimoto *et al.*, 2000; Homae *et al.*, 2002; Suzuki and Sakai, 2003). In the present study, we hypothesized that comprehension of sentences in sign language is realized in the brain in the same manner as comprehension of sentences is in the English and Japanese languages. The commonality among the modalities with regard to the left-dominant activation patterns could be properly elucidated if the language tasks given to subjects were thoroughly controlled, and if hemispheric comparisons were strictly executed.

Methods

Subjects

All of the subjects were young adults who showed right-handedness, according to the Edinburgh inventory (Oldfield, 1971). There were three groups of subjects whose L1 was either Japanese Sign Language (JSL) or Japanese (JPN): (i) Deaf signers of JSL (Deaf); (ii) hearing bilinguals of JSL and JPN (children of Deaf adults, CODA); and (iii) hearing monolinguals of JPN (Mono). The Deaf group consisted of nine congenitally profoundly deaf signers (six males, three females; ages: 22–37 years), who had binaural hearing losses of >90 dB. They had acquired JSL as their L1 from their Deaf parents (four out of nine), Deaf siblings (two out of nine) and Deaf relatives (three out of nine), who primarily used JSL. The Deaf subjects had learned JPN as L2, and had been educated orally at school. The CODA group consisted of 12 hearing bilinguals (six males, six females; ages: 19–34 years), who had acquired JSL as one of their L1s from their Deaf parents who primarily used JSL. The CODA subjects sometimes worked as interpreters in JSL and JPN. The L1 abilities in JSL for the Deaf and CODA groups were evident from the almost perfect scores they obtained on the language tasks in JSL (see Table 2). The Mono group consisted of 12 hearing monolinguals with no knowledge of JSL (seven males, five females; ages: 20–42 years), who had acquired JPN as their L1 from their hearing parents. Informed consent was obtained from each subject according to the Declaration of Helsinki. Approval for these experiments was obtained from the institutional review board of the University of Tokyo, Komaba.

Stimuli

Two sets of dialogues between two persons were prepared either in JSL or in JPN (for the entire stimuli, see Appendix 1), with exactly



Fig. 1 Examples of JSL sentences used in the Sc task. Using video-taped images of signs, we presented dialogue sentences articulated by two signers doing ‘turn-taking’ (for entire dialogues, see Appendix 1).

the same content, but with language-specific word orders and linguistic markers. Before the experiments, the subjects read through both sets of original dialogues that would appear. The dialogue sentences were articulated by two signers (a male and female) or speakers (male and female voices) doing ‘turn-taking’ (i.e. one person signs or speaks, and then the other person responds), and the dialogue continued in this manner. The rationale for using two signers/speakers was to present samples of naturalistic discourse, thereby providing contextual information through questions and answers between the two. This allows not only prosodic aspects of language to emerge, but, more importantly, discourse-level processes to be engaged, thus highlighting comprehension of sentences. Video images of the two signers were presented as JSL stimuli (resolution = 640×480 , frame rate = 30 fps), in which one signer and then the other signer presented full frontal profiles (Fig. 1). The JSL stimuli were back-projected with a liquid crystal projector onto a translucent screen placed vertically near the subject’s feet, and the subjects watched the screen through prism glasses while lying supine in the scanner and looking up at the screen.

The same JSL stimuli were presented to the Deaf and CODA groups to examine any effects associated with deafness. For the Mono group, two stimulus conditions were tested: auditory JPN stimuli alone (AUD), and the audiovisual presentation of JPN and JSL stimuli (A&V). Table 1 summarizes the four experimental conditions: Deaf, CODA, AUD and A&V. Hereafter, we refer to Deaf and CODA as the sign conditions; Deaf and CODA consisted of different subject groups, but the same JSL stimuli were used. We refer to AUD and A&V as the speech conditions; AUD and A&V were different stimulus conditions, but the same hearing monolinguals were tested.

Under the AUD condition, all speech sounds were digitized (16 bits; the normal audio cut-off, 11 025 Hz) using speech synthesis software (Oshaberi-mate, Fujitsu, Tokyo, Japan) that converted Japanese written text into digital sound waveforms. With this software, the speech stimuli faithfully replicated the prosody of speech in Japanese. The speech stimuli were presented binaurally to the

Table 1 Four experimental conditions with different subjects or different stimuli

Conditions	Subjects	Stimuli
Sign		
Deaf	Deaf	JSL
CODA	CODA	JSL
Speech		
AUD	Mono	JPN
A&V	Mono	JPN and JSL

hearing subjects through silicone-cushioned headphones specifically designed to relieve scanner noise. The maximum intensity of the stimuli was 95 dB SPL (sound pressure level) at the headphones. The subjects kept their eyes open, and viewed a cross, which was presented in the centre of an eyeglass-like MRI-compatible display (resolution: 800×600) (VisuaStim XGA, Resonance Technology, Inc., Northridge, CA). Because the Mono subjects had no knowledge of JSL, activations under the AUD condition were entirely free from JSL representations in the brain.

Under the A&V condition, the JPN and JSL stimuli were presented simultaneously, using the same sound delivery system and visual display for the AUD condition. The presentation time of each JPN stimulus was adjusted to correspond to the matching JSL stimulus by slightly changing the playback speed and the duration of silent periods. The subjects were not explicitly informed of the correspondence between the JPN and JSL stimuli. The purpose of the A&V condition was to examine the possibility that the right hemispheric activations were induced by any non-linguistic factors of merely presenting JSL stimuli, such as visuo-motor processing of signed stimuli, and the perception of facial expressions and body movements. There might be a minimal component of linguistic information in the JSL input (e.g. some lip patterns and questioning expressions in the JSL stimuli), even for non-signers. Nevertheless, we predicted that there was essentially no significant difference between the AUD and A&V

Table 2 Accuracy* of the three tasks in either sign or speech conditions

Condition	Sc	Sn	R
Sign			
Deaf	95 ± 3.4	97 ± 1.2	99 ± 0.7
CODA	97 ± 2.0	98 ± 1.4	99 ± 1.0
Speech			
AUD	96 ± 3.4	95 ± 2.6	95 ± 2.6
A&V	97 ± 1.9	95 ± 3.0	95 ± 3.1

*Mean ± SD (%).

conditions, because such fragmental pieces of information cannot lead to full comprehension of sentences for non-signers. The presentation of JSL stimuli under the A&V condition might distract from the auditory stream, reducing attention to the speech stimuli, but matched accuracy data for the three tasks under the AUD and A&V conditions (see Table 2) excluded this possibility.

Tasks

We examined two language tasks using the same sets of sentences: comprehension of sentences (Sc) task and sentential non-word detection (Sn) task. In the Sc task, the dialogue sentences were presented sequentially in the order shown in Appendix 1. In the Sn task, the sentences from the two sets of dialogues were presented in a completely randomized order; each sentence was comprehensible by itself, but it was impossible to restore a number of randomized sentences to original dialogues. One task block consisted of 5–7 sentences (2–7 s for each) and lasted for 28.3 s, including the presentation time of the name of the task (1 s) at its initiation. Detection of probe stimuli was required to ensure the subjects' full attention to the sentence stimuli. In each block of these tasks, there were always one or two probe stimuli, and the subjects were asked to respond to the probe stimuli by pressing a button. Accuracy was measured online using LabVIEW software and interface (National Instruments, Austin, TX).

In the Sc task, dialogue sentences with a probe stimulus were prepared either in JSL or in JPN (see Appendix 1). The probe stimulus belonged to the same grammatical category as the phrases it replaced, but was contextually abnormal to the dialogue. In the Sn task, the JSL probe stimuli were pseudo-sign gestures devised freely by the native signers, whereas the JPN probe stimuli were pronounceable non-words made by rearranging the order of syllables. To maintain the natural flow of sign movements, the entire sentence that included a JSL probe stimulus was performed by the same signers as if it were normal conversation. Under the A&V condition, the Mono subjects responded to the JPN probe stimuli alone, and the JSL stimuli in the Sc and Sn tasks were considered equivalent by the subjects.

Because the order of the Sc and Sn tasks was counterbalanced among the subjects, the effect of remembering the sentences from previous presentations, if any, was equivalent among the tasks. In the Sc task, participants were not making grammaticality judgements, but rather they were deciding to what extent sequences of sentences are meaningful, where individual sentences were well constructed (see Appendix 1). The crucial difference across the Sc and Sn tasks was attention to the probe stimuli at the highest discourse level versus the lower word level while processing sentences. Therefore, the Sc–Sn contrast critically taps enhanced linguistic processes at the discourse level, because more exhaustive syntactic and semantic processing was required in the Sc task than in the Sn task.

As a low-level baseline condition that sustained many of the qualities of the stimuli and tasks, but without any processing of sentences, a repetition detection (R) task was tested using video images or speech sounds used in the Sc and Sn tasks being played backward. In each block of this task, probe stimuli were one or two repetitions of an identical reversed sentence, and the subjects were asked to respond to them by pressing a button. The subjects reported that it was impossible to comprehend sentences composed of backward signs, although some of the signs were recognizable as meaningful signs, whereas no words could be recognized from backward speech. For the R task under the A&V condition, some backward signed sentences were not repeated even when backward spoken sentences were repeated, so that the subjects fully attended to the speech stimuli, but not to easily detectable repeated signs.

In a single scanning session for 254.7 s, the baseline R task and either the Sc or Sn task were presented alternately: R–Sc–R–Sn–R–Sn–R–Sc–R or R–Sn–R–Sc–R–Sc–R–Sn–R. The assignment of these two session types and that between AUD and A&V as the first session were counterbalanced among subjects. Six sessions were repeated for each condition, and one set of dialogues was completed within two Sc blocks of each session. Each of the two dialogue sets was thus repeated three times every other session, using different probes to ensure full understanding of the original dialogues.

fMRI data acquisition and analyses

The present study was performed using a 1.5 T MRI system (STRATIS II, Premium; Hitachi Medical Corporation, Tokyo, Japan). With a gradient echo echo-planar imaging sequence [repetition time (TR) = 4 s, echo time (TE) = 50.5 ms, flip angle = 90°, field of view = 192 × 192 mm², resolution = 3 × 3 mm²], we scanned 18 horizontal slices of 6 mm thickness, covering the range of $z = -48$ to 60. In a single scanning session, we obtained 64 volumes following the four dummy images, which allowed for the rise of the BOLD (blood oxygenation level-dependent) signal.

We performed group analyses with statistical parametric mapping software (SPM99; Wellcome Department of Cognitive Neurology, London, UK). Time shifts between slice acquisitions in a volume were corrected, and functional volume data were realigned further in multiple sessions. We removed sessions with a head translation of >1.5 mm in one of three directions or with a head rotation of >1.0°. Each individual brain was spatially normalized to the standard brain space as defined by the Montreal Neurological Institute (MNI), with resampling every 3 mm using sinc interpolation. These averaged data were then smoothed with an isotropic Gaussian kernel of 9 mm full width at half-maximum. Six sessions under the same condition were collapsed into one session for each subject. Task-specific effects were estimated with a general linear model (fixed effects model), and statistical parametric maps were thresholded at a corrected $P < 0.05$ at a voxel level. For observing activations, but not deactivations, in each of the intergroup comparisons, an inclusive mask for the main contrast was applied at an uncorrected $P < 0.001$; e.g. Sc–Sn, CODA as a mask for (Sc–Sn) × (CODA–Deaf). For the anatomical identification of activated regions, we used the Anatomical Automatic Labeling method (Tzourio-Mazoyer *et al.*, 2002).

Results

For each of the three tasks, the mean accuracy was always >95% (Table 2). According to an analysis of variance (ANOVA) with two variables [task (Sc, Sn, R) × group

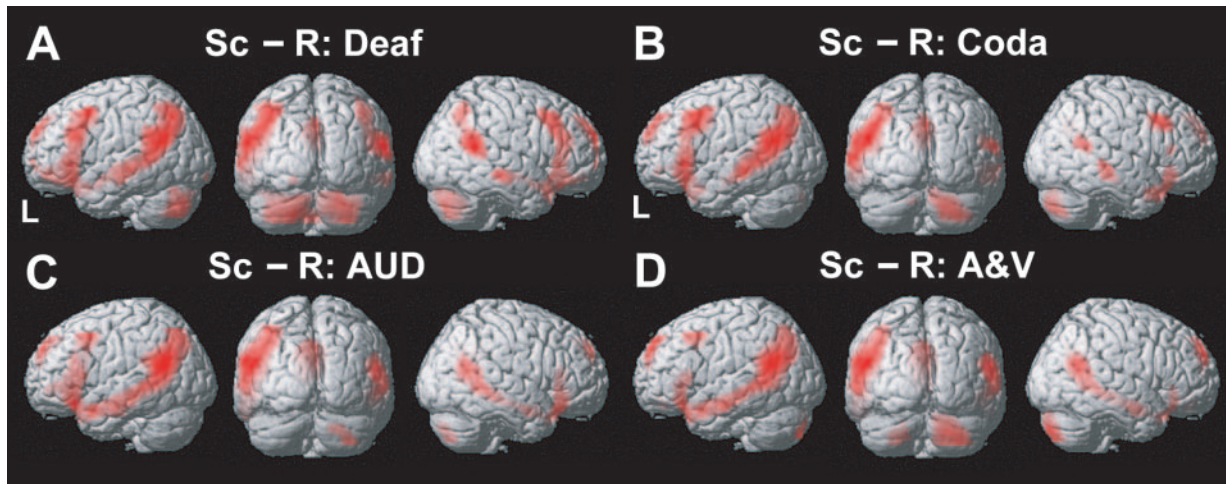


Fig. 2 Bilateral activation patterns for comprehension of sentences in sign and speech. (A–D) Cortical activations in the comparison of a comprehension of sentences (Sc) task and a repetition detection (R) task are projected onto a surface-rendered representative brain in MNI space. Significantly activated regions are shown in red (corrected $P < 0.05$). The left (L) lateral view, the posterior view and the right view are shown from the left. (A) JSL sentences were visually presented to deaf signers (Deaf). (B) JSL sentences were visually presented to hearing bilinguals (CODA). (C) JPN sentences were auditorily presented to hearing monolinguals (AUD). (D) JPN sentences were auditorily presented to hearing monolinguals, while matching JSL sentences were presented simultaneously (A&V).

(Deaf, CODA)], there were significant main effects of task. The R task was the easiest ($P < 0.0001$), but the main effects of group and interaction were not significant ($P > 0.05$). The ANOVA [task (Sc, Sn, R) \times stimulus (AUD, A&V)] showed no significant main effects or interaction ($P > 0.05$). For the two language tasks, we also compared the JSL and JPN conditions by the ANOVA [task (Sc, Sn) \times condition (Deaf, AUD)], and confirmed that there were no significant main effects or interaction ($P > 0.05$).

Figure 2 shows the results of the contrast Sc–R under the four conditions. The overall activation patterns were almost identical, in that the bilateral frontal regions, the bilateral middle temporal gyrus [MTG; Brodmann area (BA) 21], the bilateral angular gyrus (AG; BA 39), the middle occipital gyrus, the calcarine fissure and cuneus, and the bilateral cerebellum were activated. These results indicate consistent and reproducible activations among the different conditions. The frontal activation in the left hemisphere extended from the ventral inferior frontal gyrus [triangular and orbital parts (F3t/F3O); BAs 45/47] to the precentral sulcus (PrCS; BA 8). The F3t/F3O activation was observed in both hemispheres under all four conditions.

Although the results of Sc–R indicate, overall, bilateral activations under the speech and sign conditions, further voxel-wise analyses were necessary to assess the laterality of the activations quantitatively. For this purpose, cortical activations in Sc–R of the brain images flipped from side to side (i.e. mirror-reversed images derived from fMRI first-level analyses after normalization) were subtracted from the cortical activations of the normal images shown in Fig. 2. This comparison corresponds to the interaction of task and side (left versus right); the resultant activations in the left brain represent (Sc–R) \times (left–right), whereas those in the right brain represent (Sc–R) \times (right–left). Figure 3

exhibits almost identical activations in the left cerebral cortex alone under all four conditions: F3t/F3O, PrCS, MTG AG, and the inferior parietal gyrus (IPG) (see also Table 3 for the complete list of activated regions). These results clearly establish consistent left-dominant activations across all four conditions. Additional activations were observed in the left temporal pole only under the speech conditions.

Next we performed a voxel-wise ANOVA with two variables [task (Sc, Sn) \times condition (Deaf, CODA; or AUD, A&V)] separately for the sign and speech conditions. Figure 4 shows the results of the main effects of task, i.e. Sc–Sn: Deaf + CODA before Fig. 4A) and Sc–Sn: AUD + A&V (Fig. 4B). Significant activations were localized primarily in the left regions under both the sign and speech conditions: F3t/F3O, PrCS, superior frontal gyrus (F1), MTG, AG and IPG (see also Table 4 for the complete list of activated regions). Additional weaker activations were observed in the right posterior superior temporal gyrus (STG) and MTG under both conditions. It is also striking to note that the activation patterns in Sc–Sn were in good agreement with the left-dominant activation patterns in Sc–R shown in Fig. 3, indicating that the Sn task was an appropriate condition for effectively eliminating common activations in both hemispheres. We further confirmed that the following interactions resulted in no significant activation ($P > 0.05$): (Sc–Sn) \times (CODA–Deaf), (Sc–Sn) \times (Deaf–CODA), (Sc–Sn) \times (A&V–AUD) and (Sc–Sn) \times (AUD–A&V). Moreover, the equivalence for comprehension of sentences between sign and speech conditions was clearly demonstrated by the absence of significant activation in the interactions across sign and speech conditions: (Sc–Sn) \times (AUD–Deaf), (Sc–Sn) \times (AUD–CODA) and (Sc–Sn) \times (CODA–AUD). The interaction of (Sc–Sn) \times (Deaf–AUD) showed only a single small cluster of the right IPG (MNI coordinates: 45,

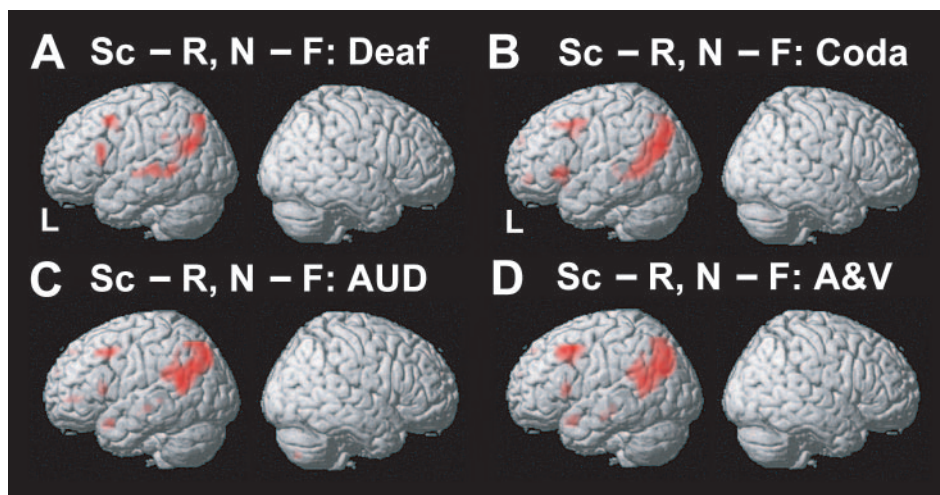


Fig. 3 Left-dominant activation patterns for comprehension of sentences in sign and speech. (A–D) Cortical activations in Sc–R of the brain images flipped from side to side (F) were subtracted from those of the normal images (N) shown in Fig. 2. The resultant activations in the left brain represent (Sc–R) × (left–right), whereas those in the right brain represent (Sc–R) × (right–left). (A) The task-by-side interaction for Deaf. (B) The task-by-side interaction for CODA. (C) The task-by-side interaction for AUD. (D) The task-by-side interaction for A&V. Note the consistent left-dominant activations across all four conditions.

Table 3 Left-dominant activations for comprehension of sentences in sign and speech

Region	BA	Side	Deaf				CODA			
			x	y	z	Z	x	y	z	Z
F3t/F3O	45/47	L	–54	18	18	6.4	–54	21	–3	7.4
PrCS	8	L	–42	9	51	>8.0	–42	3	48	7.7
F2	46	L	–42				–42	51	–3	6.5
F1	9	M					–12	60	27	4.8
MTG	21	L	–66	–30	3	7.3	–60	–51	3	7.5
AG	39	L	–42	–60	24	7.6	–45	–69	27	>8.0
SMG	40	L	–63	–39	33	4.8				
IPG	39	L	–33	–72	48	>8.0	–30	–75	48	7.7
			AUD				A&V			
			x	y	z	Z	x	y	z	Z
F3t/F3O	45/47	L	–51	18	9	5.2	–51	18	9	6.0
F3t/F2	46	L	–48	39	3	4.8				
PrCS	8	L	–42	12	45	7.8	–39	9	48	>8.0
F1	9	M	–12	45	45	5.2				
Temporal pole	38	L	–51	12	–21	6.0	–54	12	–21	7.0
MTG	21	L	–63	–24	–6	5.0	–60	–15	–15	5.1
AG	39	L	–51	–57	21	7.8	–51	–54	18	>8.0
SMG	40	L	–63	–42	24	>8.0	–63	–42	24	7.5
IPG	39	L	–36	–81	39	>8.0	–45	–72	30	>8.0
Cerebellum	–	R	36	–75	–51	5.0				

Stereotactic coordinates (x, y, z) in Montreal Neurological Institute (MNI) space are shown for each activation peak of Z values. Cortical activations in Sc–R of the brain images flipped from side to side were subtracted from those of the normal images shown in Fig. 2 (corrected $P < 0.05$); this comparison corresponds to the interaction of task and side (left versus right). Clusters smaller than 6 voxels were removed from the table for brevity. L = left; R = right; M = medial.

–60, 51; 9 voxels). These results suggest that comprehension of sentences at the discourse level enhances activations in language-related regions of the left hemisphere under both sign and speech conditions.

In contrast to the main effects of task, which resulted in activations of the left hemisphere alone (Fig. 4), the regions exhibiting the main effects of modality condition were found in both hemispheres: e.g. Sc + Sn: CODA–Deaf (Fig. 5;

see also Table 5 for the complete list of activated regions). CODA–Deaf resulted in significant activations of the left PrCS, the left precentral gyrus, the left MTG and the bilateral STG/MTG, whereas Deaf–CODA resulted in activations of the right middle frontal gyrus (F2), the right F1, the bilateral anterior STG/MTG, the right AG and the left cerebellum (Fig. 5A and B). Both AUD–Deaf and AUD–CODA showed consistent activations in the bilateral temporal pole, the bilateral posterior MTG, the calcarine fissure and cuneus, the median cingulate gyrus and the left putamen (Fig. 5C and D). On the other hand, both Deaf–AUD and CODA–AUD showed similar activations in the bilateral PrCS, the bilateral precentral gyrus, the bilateral STG/MTG and the

bilateral cerebellum (Fig. 5E and F). This result is consistent with more enhanced activation in the bilateral PrCS for Sc–R under the sign conditions than the speech conditions (Fig. 2), while maintaining the left-dominant activation of PrCS that was equivalent under both conditions (Table 3). Finally, A&V–AUD resulted in activations in the ventral F2 and the bilateral cerebellum, whereas AUD–A&V resulted in small clusters of the right F3t and the left F3t/F2 (BA 46) (Fig. 5G and H), indicating that these two conditions were essentially equivalent. Because the left F3t/F3O showed none of these main effects of modality condition, the equivalence of the left F3t/F3O activation (Figs 2 and 3) under all modality conditions was further confirmed.

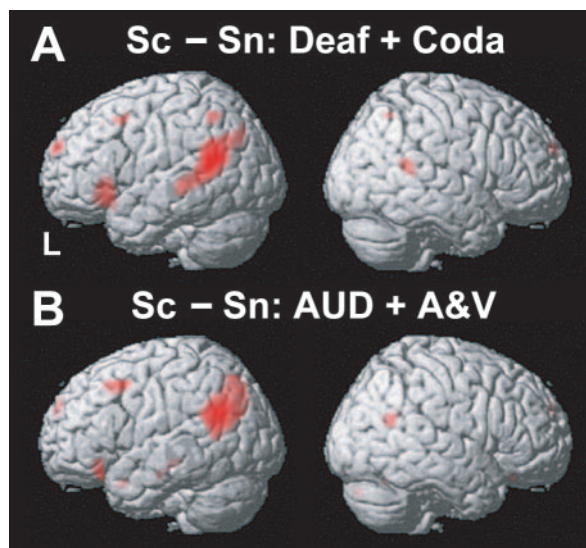


Fig. 4 Consistently enhanced activations for comprehension of sentences in sign and speech. (A and B) Activations were directly compared between the Sc task and a sentential non-word detection (Sn) task. (A) Activated regions in Sc–Sn are shown for sign conditions, where data from Deaf and CODA were combined. (B) Activated regions in Sc–Sn are shown for speech conditions, where data from AUD and A&V were combined. Note that the left-lateralized activations are equivalent for the sign and speech conditions.

Discussion

In the present neuroimaging study, we characterized and quantified the functional lateralization of cortical activations during comprehension of sentences in sign and speech. By presenting the same material for both the Sc and the Sn tasks, we could conclude that any differences in activation must be due to the recruitment of cognitive processes to the specific task, and not driven by changes in stimulus conditions or by covert processing of the material. The main results can be summarized as follows: (i) the overall bilateral activation patterns in the Sc task under the four experimental conditions of Deaf, CODA, AUD and A&V were almost identical, despite differences in stimuli (JSL and JPN) and groups (Deaf, CODA and Mono); (ii) consistently left-dominant activations involving the F3t/F3O, PrCS, MTG, AG and IPG regions were observed across all four conditions; and (iii) irrespective of the modalities of sign and speech, the main effects of task (Sc–Sn) were found primarily in the left regions: F3t/F3O, PrCS, F1, MTG, AG and IPG. Among these regions, only the left F3t/F3O showed no main effects of modality condition. While bilateral brain regions contribute to all the cognitive tasks involved, and possibly more so in sign language users, the processing of high-level language task, i.e. processing sentences, specifically activates only left frontal regions, irrespective of mode of language or hearing status. These

Table 4 Left-lateralized activations for comprehension of sentences in sign and speech

Region	BA	Side	Deaf + CODA				AUD + A&V			
			x	y	z	Z	x	y	z	Z
F3t/F3O	45/47	L	–51	24	–9	7.5	–45	30	–15	6.1
PrCS	8	L	–42	15	48	6.0	–42	12	48	>8.0
F1	9	M	–9	60	27	5.7	–15	60	30	5.8
MTG	21	L	–63	–33	–3	6.2	–63	–27	–9	5.1
STG/MTG	22/21	L	–60	–51	15	>8.0				
		R	66	–45	15	5.3	57	–60	21	5.3
AG	39	L	–45	–75	36	5.4	–51	–60	27	>8.0
IPG	39/40	L	–51	–54	51	6.3	–39	–72	51	7.1
Posterior cingulate gyrus	31	L					–3	–51	27	6.2
Cerebellum	–	R					27	–81	–33	4.7

Stereotactic coordinates are shown for each activation peak in Sc–Sn. L = left; R = right; M = medial.

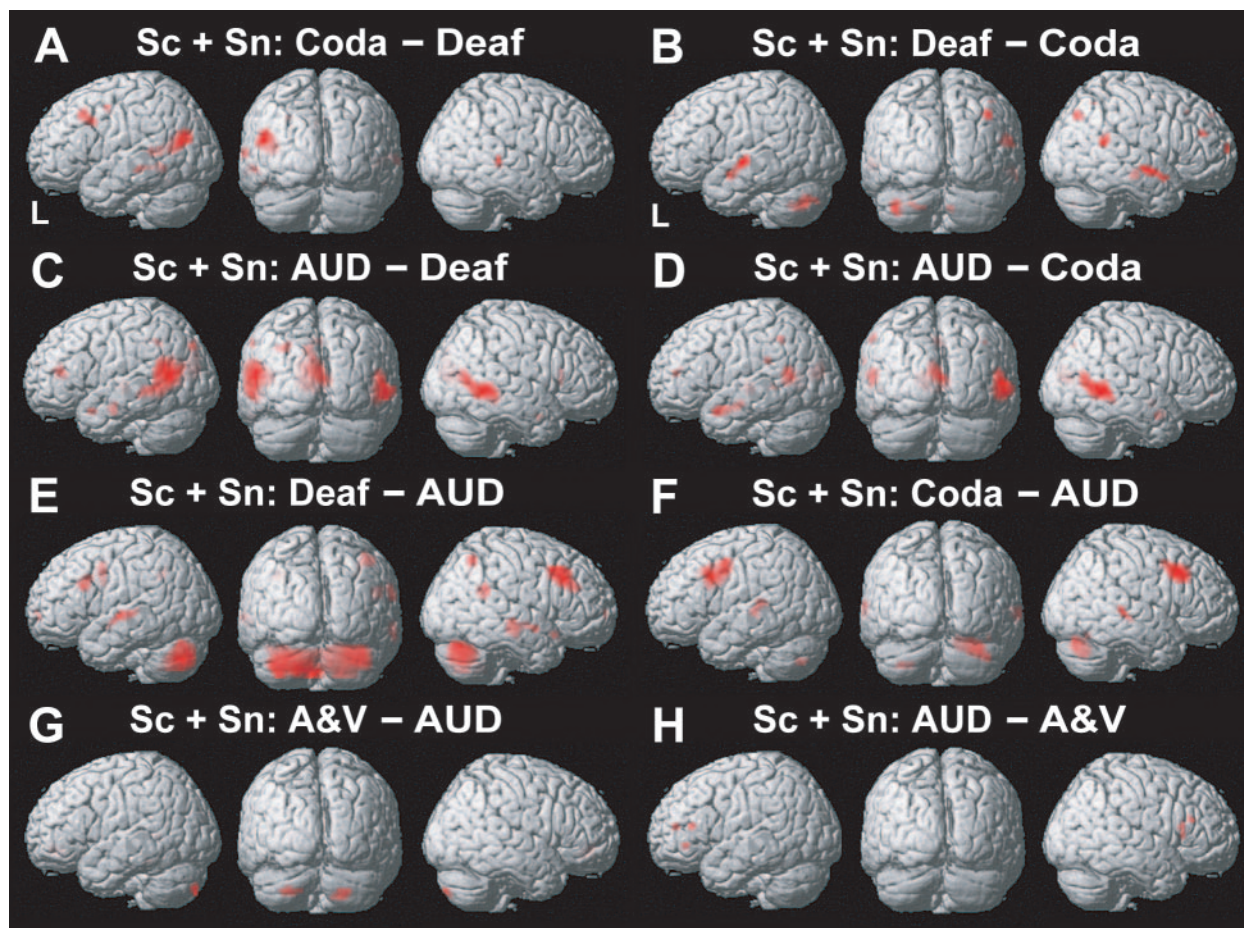


Fig. 5 Main effects of conditions among the Deaf, CODA, AUD and A&V conditions. (A–H) Cortical activations were combined for the Sc and Sn tasks, i.e. (Sc + Sn)–2R. The left (L) lateral view, the posterior view and the right view are shown from the left. The following comparisons were made: CODA–Deaf (A), Deaf–CODA (B), AUD–Deaf (C), AUD–CODA (D), Deaf–AUD (E), CODA–AUD (F), A&V–AUD (G) and AUD–A&V (H).

results demonstrate amodal commonality in the functional dominance of the left cortical regions for comprehension of sentences, as well as the essential and universal role of the left F3t/F3O.

On the issues of functional lateralization of the two hemispheres, we propose that functional lateralization is not an all-or-none phenomenon (e.g. left but not right), but that it reflects dominance of one hemisphere over the other, the salience of which can be modulated parametrically by task demands. In the present study, left-dominant activations were clearly exhibited in the Sc task, even if bilateral activations existed under the same conditions, as confirmed by the comparison with the lowest level R task (Figs 2 and 3). Moreover, we clarified that this dominance is related to specific linguistic factors in the Sc task, as demonstrated by the comparison with the Sn task (Fig. 4). Therefore, it turns out that the choice of task is critical in determining and comparing cerebral dominance. The left F3t/F3O activation in the present study is consistent with the activations in sign production tasks for Deaf subjects reported by Petitto *et al.* (2000). However, it is difficult to interpret, from the results of that study, why the right F3t/F3O was significantly activated

when the verb generation task was compared with an imitation task, but not when the same verb generation task was compared with a less stringent fixation task. In contrast, we observed the right F3t/F3O activation under all four conditions only when the Sc task was compared with the R task, but not when it was compared with the more stringent Sn task. Thus, it is crucial to employ appropriate task comparisons for proper evaluation of the weaker activations in the right hemisphere.

Processing sentences involves the integration of syntactic and lexico-semantic information, constrained in part by short-term memory resources (Gibson and Pearlmuter, 1998). As a result of this integration, sentences convey not only lexico-semantic information for each word, but sentence meaning based on syntactic structures (Caplan, 1992; Townsend and Bever, 2001; Friederici, 2002; Sakai *et al.*, 2003). Even though such automatic sentence processing probably occurs in both Sc and Sn tasks, the Sc task explicitly requires such selection and integration of semantic information across sentences for understanding and tracking the contextual information within the dialogues. In our previous study, we directly contrasted a sentence (S) task, which is similar to the Sc task,

Table 5 Main effects of conditions among the Deaf, CODA, AUD and A&V conditions

Region	BA	Side	CODA–Deaf				Deaf–CODA			
			x	y	z	Z	x	y	z	Z
PrCS	8	L	–42	21	42	7.0				
Precentral gyrus	6	L	–45	0	51	5.6				
F2	46	R					45	45	24	5.1
F1	10	R					24	66	12	6.4
STG/MTG	22/21	L	–66	–42	9	5.3	–57	–12	0	7.7
		R	66	–33	3	5.3	63	–6	–6	6.9
		R					57	–48	18	5.3
MTG	21	L	–57	–42	–6	5.8				
			–48	–72	21	7.6				
AG	39	R					39	–75	39	5.6
Cerebellum	–	L					–42	–72	–39	7.0
			AUD–Deaf				AUD–CODA			
			x	y	z	Z	x	y	z	Z
F2	46	L	–48	39	15	6.4				
Temporal pole	38	L	–54	12	–21	5.5	–54	6	–21	6.6
		R					54	3	–24	5.6
MTG	21	L	–60	–9	–21	5.8				
		L	–54	–57	15	>8.0	–54	–57	12	5.9
		R	60	–48	–3	>8.0	60	–48	0	>8.0
IPG	40	L					–54	–51	48	5.2
Middle occipital gyrus	19	L	–30	–84	39	5.8				
Lingual gyrus	19	M					9	–63	3	6.0
Calcarine fissure/cuneus	17/18	M	–12	–60	6	>8.0	3	–84	9	6.6
Median cingulate gyrus	31	M	3	–42	45	7.1	3	–42	45	6.2
Putamen	–	L	–33	–18	0	6.9	–33	–18	0	7.2
		R					30	–6	–9	6.1
			Deaf–AUD				CODA–AUD			
			x	y	z	Z	x	y	z	Z
PrCS	8	L	–54	18	30	6.8	–42	18	39	5.8
		R	42	24	39	7.7	54	12	36	>8.0
Precentral gyrus	6	L	–51	3	42	6.5	–45	0	51	>8.0
Temporal pole	38	R	51	15	–15	5.0				
STG/MTG	22/21	L	–63	–12	0	>8.0	–66	–24	3	7.5
		R	66	–21	–9	>8.0	69	–30	0	7.1
AG	39	R	51	–51	24	5.3				
IPG	39/40	L	–33	–54	39	5.2				
		R	45	–57	51	5.5				
Cerebellum	–	L	–36	–72	–36	>8.0	–30	–66	–45	5.2
		R	39	–69	–33	>8.0	30	–66	–30	7.6
		M	–3	–57	–45	6.5				
			A&V–AUD				AUD–A&V			
			x	y	z	Z	x	y	z	Z
F3t	45	R					60	18	15	4.9
F3t/F2	46	L					–42	36	–3	4.8
		L					–45	33	15	4.7
F2	10	M	3	42	–6	5.4				
Cerebellum	–	L	–27	–84	–42	5.2				
		R	21	–84	–45	5.1				

Stereotactic coordinates are shown for each activation peak in the contrasts indicated. Cortical activations were combined for the Sc and Sn tasks, i.e. (Sc + Sn)–2R. L = left; R = right; M = medial.

with a phrase (P) task, in which phrases taken from dialogues were presented in a completely randomized order and subjects were asked to detect non-words among them (Homae *et al.*, 2002). In spite of the general impression that discourse processing requires bilateral regions of the brain, we have already established that the left-lateralized activation in F3t/F3O is selective to processing sentences at the discourse level, irrespective of the modalities of speech sounds and written words. Furthermore, we recently reported that the reciprocal connectivity between the left F3t/F3O and the left PrCS is significantly enhanced during the S task, but not during the P task (Homae *et al.*, 2003). In the present study, we successfully observed significant activation of the left F3t/F3O with the more highly stringent comparison of Sc–Sn, where sentence stimuli were presented in both conditions, than with the previous comparison of S–P. Combining these results, we have established that the network of the left F3t/F3O and the left PrCS is consistently involved in comprehension of sentences, irrespective of the modalities of signs, speech sounds and written words. Moreover, this is true for monolingual or bilingual subjects, even if some research on spoken language bilingualism has argued that there is always dominance of one language over another (Perani *et al.*, 1998).

The equivalent results between the Deaf and CODA groups in the present study further established that the left dominance in cortical activations (Figs 3 and 4) can be independent from the status of hearing. This observation is important from neurological points of view, and fits well with the existing functional imaging studies that have reported similar activations between Deaf and hearing native signers (Neville *et al.*, 1998; MacSweeney *et al.*, 2002b). The bilateral posterior MTG activation observed in CODA–Deaf (Fig. 5A) may reflect automatically translating the JSL stimuli into JPN for the CODA subjects, because the MTG activation was more clearly observed in both AUD–Deaf and AUD–CODA (Fig. 5C and D), selective to the speech condition. In contrast, Deaf–CODA (Fig. 5B) showed unexpected activations in the bilateral anterior STG/MTG. MacSweeney *et al.* (2002b) have also reported greater activation for Deaf native signers than hearing native signers in the left STG (Talairach coordinates: –49, –36, 12), although this locus does not exactly coincide with ours (Table 5). The bilateral cerebellum activation in Deaf–CODA may be due to enhanced visuo-motor processing of signed stimuli for the Deaf subjects, because the cerebellum activation was more prominent in both Deaf–AUD and CODA–AUD (Fig. 5E and F), selective to the sign condition. The bilateral cerebellum activation in A&V–AUD (Fig. 5G) is also consistent with this interpretation. Consistent with other activated regions in Deaf–AUD and/or CODA–AUD, a recent fMRI study with BSL has also reported the bilateral activations in PrCS (BA 44), IPG (BA 39/40) and the posterior MTG (BA 21/37), when comprehension of topographic sentences (i.e. expression of spatial relations) was compared with that of non-topographic sentences (MacSweeney *et al.*, 2002a). These activation

patterns with the modality effects were mostly bilateral, in contrast to the clearly left-lateralized activations for the Sc task. It should also be noted that the right F3t/F3O activation did not differ significantly between the Sc and Sn tasks (Figs 2 and 3), suggesting that cognitive factors, such as the prosody commonly involved in these tasks, were sufficiently effective to cause the right F3t/F3O activation.

The functional lateralization of F3t/F3O found in Sc–Sn under both sign and speech conditions further establishes that the recruitment of this region for comprehension of sentences is universal among natural languages. It is consistent with the accumulating evidence that aphasia in signed language is primarily due to left-hemisphere lesions, just like aphasia in spoken language (Poizner *et al.*, 1987; Bellugi *et al.*, 1989). Moreover, theoretical models of sentence comprehension, even though they are either rule-governed or habit-based models, do not depend explicitly on the constraints of modality (Frazier, 1987; McClelland *et al.*, 1989; Mitchell, 1994; Townsend and Bever, 2001). The present study thus contributes to resolving the ongoing debate about lateralization of sign language processing by clarifying, for the first time, that the left F3t/F3O subserves comprehension of sentences, irrespective of the language modalities.

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Appendix 1: English translations of JSL/JPN discourse stimuli

Dialogue No. 1 (Sentences with a probe stimulus are italicized.)

- A (a man): When will the next Deaf Society meeting be held?
 B (a woman): It will be held in Ishikawa next July.
(It was held in Ishikawa last July.)
 A: Oh, I see. How can I register for it?
(Oh, I see. How can I escape it?)
 B: Are you a member of the Deaf Society?
(Are you a member of the Sports Society?)
 A: No, I'm not a member.
(No, I'm not a student.)
 B: I see. You can't register for it unless you are a member.
(You can't register for it if you are a member.)
 A: Then I'll become a member.
(Then I'll become a teacher.)
 B: Now, please fill in this form.
 A: OK. How much is the fee?
(OK. How much is the debt?)
 B: 140 dollars per year for a regular member.
(140 dollars per day for a regular member.)
 A: That's a lot. I don't have the money now. What should I do?
(That's hot. I don't have the money now. What should I do?)
 B: No problem. Could you bring the money to this office?
(No problem. Could you bring the money to this jail?)
 A: Sure. I'll come again next Tuesday.
(No. I'll come again next Tuesday.)

Dialogue No. 2 (Sentences with a probe stimulus are italicized.)

- A (a man): Have you ever been to the States?
 B (a woman): Yes, I have been there three times.
(Yes, I have eaten them three times.)
 A: Oh, I see. What have you been for?
(Oh, I see. What have you come for?)
 B: Well, for business one time. For sight-seeing the other two times.
(Well, for exercise one time. For sight-seeing the other two times.)
 A: I see. Where did you go for your sight-seeing?
(I see. Where did you go for your trial?)
 B: Mostly on the west coast. I went to Los Angeles and Seattle.
(Mostly on the west coast. I went to India and Seattle.)
 A: Really? My sister lives in Seattle.
 B: I see. Is your sister Deaf, too?
(I see. Is your sister a woman, too?)
 A: Yes, she is. She is married to a Deaf American.
(Yes, she is. She is dining with a Deaf American.)
 B: I see. I'll be visiting the States again, so please tell her about me.
(I see. I'll be visiting the States again, so please leave her.)
 A: With pleasure. She will like that too.
(With pleasure. She will laugh, too.)
 B: Thank you so much.