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Hemispheric specialization for English and ASL: left invariance-right variability

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FUNCTIONAL magnetic resonance imaging (fMRI) was used to compare the cerebral organization during sentence processing in English and in American sign language (ASL). Classical language areas within the left hemisphere were recruited by both English in native speakers and ASL in native signers. This suggests a bias of the left hemisphere to process natural languages independently of the modality through which language is perceived. Furthermore, in contrast to English, ASL strongly recruited right hemisphere structures. This was true irrespective of whether the native signers were deaf or hearing. Thus, the specific processing requirements of the language also in part determine the organization of the language systems of the brain *NeuroReport* 9: 1537–1542 © 1998 Rapid Science Ltd.

Key words: fMRI; Hemispheric specialization; Neurobiology of language; Plasticity; Sentence processing; Sign language

Introduction

Two competing hypotheses are often brought forward to account for the linguistic specialization of the left hemisphere. Several authors have proposed that the left hemisphere is neurologically set to process and generate fast acoustic transitions, and thus affords a special role in language processing.[1] The apparent co-evolution of language with the differentiation of the neuro-anatomical mechanisms involved in the motor control of speech production lend additional support to the view that the language specialization of the human brain is driven by speech.[2] In contrast, others have suggested that the grammatical recoding of sensory information which is necessary for language processing drives left hemisphere specialization.[3,4] Observations that the degree of left hemisphere lateralization for language co-varies with grammatical competence have led a number of authors to propose that grammatical proficiency is one of the major factors underlying left hemisphere specialization for language.[5,6] While these two hypotheses are not mutually exclusive, their relative role is difficult to assess when studying solely aural-oral languages. The use of a visuo-manual language such as American sign language (ASL) offers a unique opportunity to test the relative roles of these two factors in the cerebral organization for language. While the use of ASL requires grammatical recoding, it relies upon visual inputs and thus makes little or no demands on auditory processing.[7] In addition, the duration of linguistically significant temporal contrasts for spoken and signed languages differ dramatically, thus providing an opportunity to explore the role of processing time constraints on language lateralization.[8]

Left hemisphere damage has been reported to lead to similar language deficits in patients whose first language is ASL and in patients whose first language is English.[9,10] Thus, the sound-based processing which is typical of natural languages may not be necessary for the specialization of the left hemisphere. However, whether cortical organization for ASL is similar to that for English is still an open question.

Moreover, there is limited and contradictory evidence on the proposal that the right hemisphere may play a role in processing ASL.[9,11,12] In order to address these issues, we compared cortical organization for written English in hearing native speakers to that for ASL in deaf native signers. To control for the effects of deafness, we also studied normally hearing subjects who acquired ASL as a native language. A summary of the language experience of each population is given in Table 1. The fMRI technique was used to image each population while processing sentences in their native language, English for hearing native speakers and ASL for both deaf and hearing native signers. All stimuli were presented visually. The English runs consisted of blocks of sentences that alternated with blocks of consonant strings. The ASL runs consisted of blocks of film of a native signer producing sentences in ASL that alternated with blocks of film of the same signer producing non-sign gestures physically similar to signs. At the end of each run, subjects had to perform a yes/no recognition task on the stimuli they had just viewed. The behavioral data indicated that subjects were attending to the stimuli and were better at recognizing sentences than nonsense strings/signs (English, hearing $F(1, 15) = 46.9, p < 0.00001$; ASL, deaf $F(1,23) = 18.8$, $p < 0.0003$; ASL, hearing signer $F(1, 18) = 61.5, p < 0.00001$; see also Table 1). Each population performed equally well in their respective natural language (no group effect, $p > 0.1$).

Materials and Methods

Subjects: All subjects were right-handed, healthy adults with no known neurological abnormalities (see Table 1).

MR scans: Gradient-echo echo-planar images were obtained using a 4T whole body MR system, fitted with a removable z-axis head gradient coil.[13] Eight parasagittal slices, positioned from the lateral surface of the brain to a depth of 40 mm, were obtained (TR = 4 s, TE = 28 ms, resolution 2.5 × 2.5 × 5 mm, 64 time points per image). For each of the subjects, only one hemisphere was imaged in a given session since a 20 cm diameter transmit receive radio-frequency surface coil was used. Structural scans, corresponding to the functional scans, were also acquired during each session (GRASS sequence, 256 × 256 pixels, TR = 200 ms, TE = 10 ms, flip angle = 15°).

Experimental design/stimulus materials: The English runs consisted of alternating blocks of simple declarative sentences (read silently) and consonant strings, all presented one word/item at a time in the center of a screen at a rate of 600 ms/item. The ASL runs consisted of similar alternations of simple ASL sentences and non-sign gestures that were physically similar to ASL signs. ASL sentences and non-sign gestures were produced by the same deaf native signer. The material was presented in four different runs (two of English and two of ASL presentation counterbalanced across subjects). Each run consisted of four cycles of alternating 32 s blocks of sentences (English or ASL) and baseline (consonant strings or nonsigns). None of the stimuli were repeated. Subjects had a practice run of ASL and of English to become familiar with the task and nature or the stimuli.

Behavioral tests: After each run, subjects were presented sequentially with six sentences and six non-words/non-signs. For each of these twelve test stimuli, they indicated to the experimenter whether those had appeared in the run or not by raising either their left or right hand (see Table 1). Half of the test stimuli had appeared before and half were new. ANOVAs were performed on the log transform of the percent correct yes/no recognition.

MR analysis: Subjects were asked to participate in two separate sessions (one for each hemisphere). However this was not always possible, leading to the following numbers of subjects: (A) hearing: eight

Table 1. Demographic and behavioral data.

	Hearing	Congenitally deaf	Hearing native signers
Native language	English	ASL	English and ASL
Hearing	Normal	Profound deafness	Normal
Mean age (years)	26	23	35
Handedness	Right	Right	Right
Language conditions of interest	English	ASL	ASL
% correct on recognition task			
Sentences	85 ± 2.5	92 ± 1.9	92 ± 1.9
Non-words/non-signs	52 ± 3.9	62 ± 2.5	60 ± 2.8
Number of subjects (runs)			
Left hemisphere	8 (13)	11 (17)	8 (12)
Right hemisphere	8 (15)	12 (21)	10 (17)

subjects on both left and right hemispheres, (B) deaf: seven subjects on both left and right hemispheres, plus four subjects left hemisphere only and five subjects right hemisphere only, (C) hearing native signers: six subjects on both left and right hemisphere, plus three subjects left hemisphere only and four subjects right hemisphere only. Individual data runs were first checked for artifacts (runs with visible head motion and/or signal loss were discarded from the analysis, resulting in the loss of data from four hearing native signers – two for left hemisphere on English, one for left hemisphere on ASL and one for right hemisphere English). A cross-correlation thresholding method was used to determine active voxels[14] ($r \geqslant 0.5$, effective $df = 35$, alpha = 0.001). The Rademacher *et al.*[15] division of the lateral surface of the brain was used to delineate, on each MR structural image, the two regions of interest (inferior frontal-Broca's area, BA 44-45, [ahr-anterior horizontal ramus, F3t-inferior frontal gyrus/pars triangularis, aar-anterior ascending ramus, F30-inferior frontal gyrus/pars opercularis], posterior temporal-Wernicke's, BA 22 [superior temporal sulcus at T1p/T2p junction[15]]) as well as the extension of this posterior temporal region to adjacent temporo-parietal cortex, BA 39 (angular sulcus [ag] and anterior occipital sulcus [ao]). Between-subjects analyses were performed on these anatomical regions using multivariate statistics. Activation measurements were made on the following two variables for each region and run: (a) the mean percent change of the activation for active voxels in a region and (b) the mean spatial extent of the activation in the region (corrected for size of the region). In all analyses, the log transform of these two variables were used as dependent variables, and runs as the independent variable. The analyses relied on Hotelling's T2 statistic, a natural generalization of Student's *t*-statistic to multiple dependent variables, and were performed using BMDP Statistical Software.[16] Activation within a region was assessed by testing the null hypothesis that the level of activation in the region is equal to zero. Comparisons across hemispheres and/or groups were performed by entering these as between-subject factors (see Ref. 17 for further details).

Results

The level of activation within each of the regions of interest was assessed by performing MANOVAs on percentage change and mean spatial extent region by region. Hearing and deaf showed robust activation within left hemisphere regions (Broca's: hearing $F(2,11) = 17.1$, $p < 0.0004$; Deaf, $F(2,15) = 8.3$, $p < 0.0043$; Wernicke's: hearing, $F(2,11) = 40.6$, $p < 0.00001$; deaf, $F(2,11) = 9.3$, $p < 0.0023$). Activation in the right hemisphere was more variable across groups (Broca's: hearing, $F(2,13) = 4.2$, $p < 0.039$; deaf, $F(2,19) = 11.9$, $p < 0.0004$; Wernicke's: hearing, $F(2,13) = 2.3$, $p > 0.1$; deaf, $F(2,19) = 29.0$, $p < 0.00001$). Comparison of left and right hemisphere activation established a left hemisphere dominance for hearing (Broca's: $F(2,25) = 5.4$, $p < 0.0112$; Wernicke's: $F(2,25) = 13.0$, $p < 0.0001$) but not for deaf (Broca's: $F(2,35) = 0.08$, $p > 0.9$; Wernicke's: $F(2,35) = 0.88$, $p > 0.4$). A MANOVA analysis with group and hemisphere as factors revealed group by hemisphere interactions for each of the areas considered (Broca's: $F(2,61) = 3.8$, $p < 0.028$; Wernicke's: $F(2,61) = 9.52$, $p < 0.0003$), confirming different lateralization for English and ASL. These results are summarized in Table 2.

Assessment of the relative contribution of deafness and early acquisition of ASL was assessed by studying hearing native signers. As in deaf signers, posterior right areas were robustly active (Table 2). Recruitment of right temporo-parietal areas in native signers was further studied by extending our study of the posterior temporal region to the adjacent angular sulcus and horizontal sulcus. Robust activation was observed for deaf and hearing native signers in these right hemisphere areas (angular sulcus: deaf, $F(2,19) = 14.2$, $p < 0.00001$; hearing signer, $F(2,15) = 16.7$, $p < 0.0002$; anterior occipital sulcus: deaf, $F(2,19) = 7.8$, ps< 0.0035; hearing signer, $F(2,15) = 8.5$, $p < 0.0035$). By contrast, none of these areas was robustly active during English processing in native speakers (ps > 0.07). MANOVAs over the three temporo-parietal regions comparing each population of native signers to native speakers revealed significantly more activation for signers than speakers (ASL-deaf/English-hearing $F(2,101) = 13.98$, $p < 0.00001$; ASL-hearing signer/English-hearing $F(2,89) = 13.96$, $p < 0.00001$).

Discussion

The hypothesis that left hemisphere structures are recruited independently of the nature and modality of the natural language acquired was tested by assessing the recruitment of the two classical language structures (inferior frontal-Broca's and posterior temporal-Wernicke's areas) when hearing native speakers read English sentences and when deaf native signers viewed ASL sentences. Figure 1 summarizes the pattern of activation for each group. The finding that hearing native speakers displayed robust activation within each of these areas when reading English sentences is consistent with the wealth of literature documenting the participation of these areas in aural–oral language.[18,19] Our results, however, clearly show that inferior frontal-

Table 2. Significance levels, percentage subjects and percentage runs with activation in the left hemisphere and in the right hemisphere for English-hearing, ASL-deaf and ASL-hearing native signers. The third column displays the interaction between left and right hemisphere activation. A left hemisphere advantage is noted by (L).

	Activation in left hemisphere			Activation in right hemisphere			Hemisphere effect
English (hearing native speakers)	*p*	% Subjects	% Runs	*p*	% Subjects	% Runs	*p*
IF-Broca's	0.0004	75	77	0.0387	50	40	0.0112 (L)
PT-Wernicke's	0.0000	100	92	0.1434	50	27	0.0001 (L)
ASL (deaf native signers)	*p*	% Subjects	% Runs	*p*	% Subjects	% Runs	*p*
IF-Broca's	0.0043	64	53	0.0004	75	62	0.9227
PT-Wernicke's	0.0023	73	59	0.0000	83	81	0.4248
ASL (hearing native signers)	*p*	% Subjects	% Runs	*p*	% Subjects	% Runs	*p*
IF-Broca's	0.0008	87	83	0.0379	60	41	0.0011 (L)
PT-Wernicke's	0.0003	75	83	0.0002	80	71	0.2837

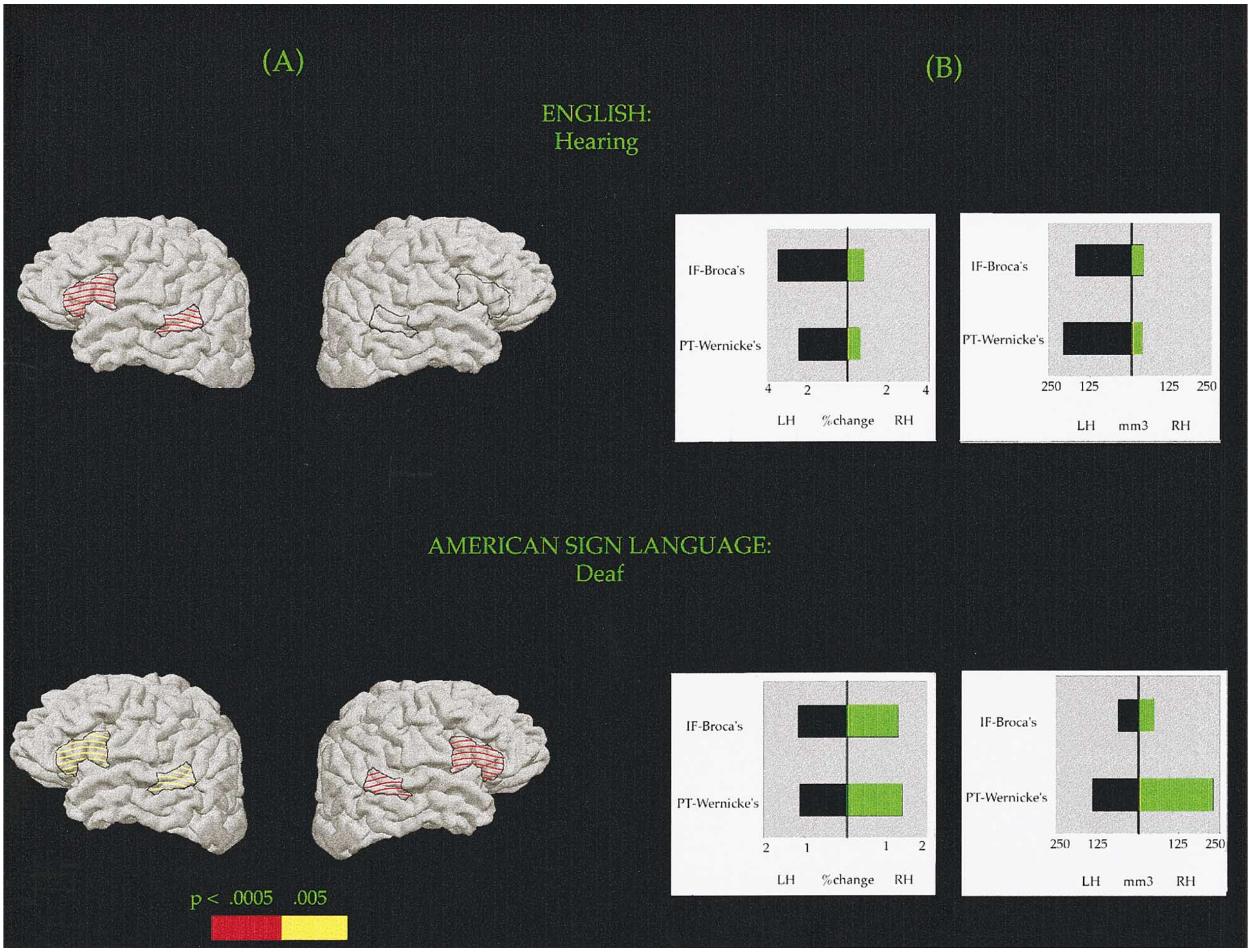

FIG. 1. (**a**) Significance levels in anatomical regions of interest displayed on a 3D-reconstructed template brain. (**b**) Average percentage change and average active volume for each anatomical region of interest. IF = inferior frontal; PT = posterior temporal.

Broca's and posterior temporal-Wernicke's areas were also robustly recruited in deaf native signers processing ASL. Activation within these areas in deaf individuals with no auditory experience and whose native language is a visual spatial language, suggests the left hemisphere specialization for language cannot arise solely from a bias to process rapidly presented auditory information. Rather our results are consistent with the view that recruitment of these left hemisphere structures is dependent on the acquisition and mastering of a natural (grammatical) language early in development.[6,19–20]

The role of the right hemisphere in language processing as a function of language modality was assessed by studying the pattern of activation in the right hemisphere areas homologous to the classical left language areas considered above. Our results show that while hearing native speakers displayed no robust activation in these right hemisphere areas when reading English, deaf native signers displayed highly significant right hemisphere activation when viewing SL. This difference in right hemisphere recruitment resulted in strikingly different patterns of lateralization for each language group. In accordance with previous studies, the activation was left lateralized in hearing native speakers (Table 2, all p values for hemisphere effects < 0.015). By contrast, no lateralization effects were observed in deaf native signers (all p values for hemisphere effects > 0.4). The finding of a group by hemisphere interaction for each of the areas considered confirmed different lateralization for English and ASL.

The possibility that auditory deprivation, rather than language modality, contributed to this pattern of results was assessed by studying cortical organization for ASL processing in hearing native signers (see Table 1 for a description of the language experience of this population). As can be seen in Table 2, these subjects displayed an activation pattern similar to that observed in deaf native signers viewing ASL, including the recruitment of the inferior frontal-Broca's and posterior temporal-Wernicke's areas in the left hemisphere and robust activation in the right hemisphere homologue of the posterior temporal-Wernicke's area. Thus, in the left hemisphere, inferior frontal-Broca's and posterior temporal-Wernicke's areas were recruited during English processing in native speakers as well as during ASL processing in native signers (whether deaf or hearing) indicating that the recruitment of the classical left hemisphere areas is robust across different language modalities and experience.

While classical left hemisphere areas were found active across language modality, activation in the right hemisphere was found to be affected by the nature of the language. Indeed, reliable activation of posterior right hemisphere areas was present in native signers, whether deaf or hearing, but not in native English speakers suggesting that the recruitment of these areas is determined by the demands of ASL processing rather than by the availability of auditory experience. This finding was further confirmed by extending the region of interest to adjacent temporoparietal cortex (angular sulcus/anterior occipital sulcus).[15] Robust activation was observed for deaf and hearing native signers in these right hemisphere areas, but not during English processing in native speakers. Group comparisons revealed significantly more activation for signers than speakers in these areas. In accordance with our findings, recent electrophysiological studies of neurologically intact native signers also indicate that the right hemisphere is active during ASL sentence processing.[12] Given the well documented role of the right hemisphere in visuo-spatial processing,[21] it is tempting to conclude that the participation of these posterior right areas are due to increased visuo-spatial processing during ASL viewing. However, areas active for ASL were those areas which displayed activation above our control condition in which a deaf native signer was viewed executing arbitrary hand and face motions. Since both the ASL and the control condition required spatial processing, the right hemisphere recruitment observed in this study cannot be easily accounted for by spatial information in the visual input per se. Moreover, subjects that were not familiar with ASL displayed no difference in activation between viewing these two conditions suggesting that the ASL and control gestural sequences were closely matched in terms of sensory visuo-spatial information.[17] Finally, the right hemisphere activation observed in our study is more inferior and lateral than the right hemisphere areas activated during the perception of meaningless gestures.[22] We speculate that the right hemisphere activation in native signers is linked to the linguistic use of space required in ASL,[7] and not visuo-spatial processing per se. While this claim is consistent with recent studies of signers with right hemisphere lesions indicating disruptions in those aspects of ASL which make exceptional demands on spatial processing,[11] it will require future research to assess the functional significance of the right hemisphere recruitment we report.

Conclusion

Taken together, our results show that inferior frontal-Broca's and posterior temporal-Wernicke's areas within the left hemisphere are recruited when both deaf and hearing individuals are engaged in processing their native language (ASL or English). These results show that the processing of fast acoustic transitions is not necessary for recruitment of the left hemisphere structures in the language system. In contrast, the left hemisphere invariance across languages is consistent with the view that grammatical recording drives the left hemisphere specialization for language. However, further evidence will be required to demonstrate that the active areas support similar functions across languages. The finding of a different right hemisphere recruitment for English and ASL raises the possibility that some aspects of language processing can also drive a right hemisphere specialization for language. While a finer assessment of the functional role of right hemisphere structures is required, the difference in lateralization pattern between English and ASL reported in the present paper establishes that the cerebral organization for language can be altered by the structure and processing requirements of the language.

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