Brain Organization: Clues from Deaf Signers with Left or Right Hemisphere Lesions

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BRAIN ORGANIZATION: CLUES FROM DEAF SIGNERS WITH LEFT OR RIGHT HEMISPHERE LESIONS

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INTRODUCTION.

The central issues that we address arise from some discoveries about the nature of language. Until recently, nearly everything known about language came from the study of spoken languages. Now, research has revealed that there are signed languages that are primary linguistic systems passed down from one generation of deaf people to the next which have become forged into separate languages, not derived from spoken languages. Thus, for the first time we can examine properties of communication systems that have developed in alternate transmission systems. The existence of these fully expressive systems affords a new vantage point for investigating the nature of the biological underpinnings of language and cognition, and the study of deaf signers with left or right hemisphere damage provides an unusual opportunity for investigating brain organization for language. Sign languages clearly present test cases for theories about the nature of language and the determinants of brain organization for language. We have specified the ways in which the formal properties of languages are shaped by their modalities of expression, sifting properties peculiar to a particular language modality from more general properties common to all languages. ASL exhibits formal structuring at the same levels as spoken languages, and contains similar kinds of organizational principles. But at all structural levels the form of an utterance in sign is deeply influenced by the modality in which the language is cast. The most striking surface difference between signed and spoken language is the reliance on spatial contrasts at all linguistic levels, evident at the level of ASL grammar and also in extrasyntactic functions such as discourse. This spatialized organization is a unique property of visual-gestural systems.

It has been long established that the left cerebral hemisphere if dominant for speech and the processing of grammar, and that the right hemisphere is dominant for many aspects of spatial processing. But until recently the nature of brain organization for sign language had been relatively unexplored. This issue is interesting because sign languages exhibit properties for which each of the hemispheres of hearing people shows a different predominant functioning; thus the study of brain-damaged signers provides clues to higher cognitive functions in the brain, and how modifiable that organization may be. These studies also make important contributions to awareness of the needs of deaf people and the development of therapies for those who have suffered brain damage.

The central question we address in our research program (“Brain Organization: Clues from Sign Aphasia”) is the extent to which the functional neuroanatomy of language is dependent on the sensory and motor modalities through which it is perceived and produced. There are many reasons to think that the neural organization of language should be profoundly influenced by extrinsic factors in development such as sensory and motor experience. The temporal processing demands imposed by the auditory system have been argued to favor left hemisphere systems which could, in turn, determine aspects of the lateralization pattern of auditory-mediated language. Superior temporal lobe regions thought to be important for language comprehension are situated in and around auditory cortices -- a natural location given auditory sensory input of language. Likewise, Broca's area, which is thought to play a role in speech production, is situated just anterior to motor cortex controlling the speech articulators. Thus, it would not be unreasonable to hypothesize that the neural organization of language -- including its lateralization and within hemisphere organization -- is determined in large part by the particular demands imposed by the sensory and motor interface systems.

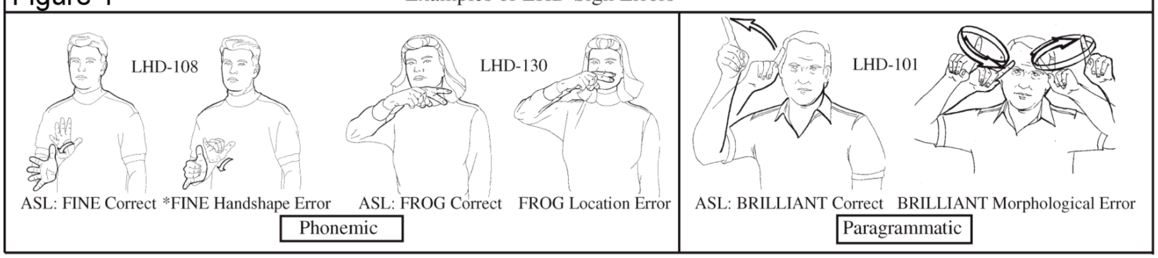
By studying the functional neuroanatomy of signed language, we can test this hypothesis in a straightforward manner. It has been shown that signed languages share much of the formal linguistic structure found in spoken languages, but differ radically in the sensory and motor systems through which language is transmitted (Bellugi & Klima, 2001; Emmorey, 2002). In essence, signed language offers a kind of natural experimental manipulation: central linguistic structure and function are held constant, while peripheral sensory and motor experience is varied. Thus, a comparison of the neural organization of signed versus spoken language will provide clues concerning factors which drive the development of the functional neuroanatomy of language. In the course of this research program, we have made substantial progress in understanding the neural basis of sign language, and our findings have sparked interest -- indeed active research programs -- in several other labs. Here we will provide a brief report on the progress we have made in last five years.

HEMISPHERIC ASYMMETRIES FOR GRAMMATICAL AND SUBLEXICAL ASPECTS OF ASL

Left hemisphere damage (LHD) in hearing/speaking individuals is associated with deficits at sublexical ("phonetic/phonemic"), lexical, and sentence levels, both in production and in comprehension (Damasio, 1992). Right hemisphere damage (RHD), on the other hand, has been associated with supra-sentential (e.g., discourse) deficits. Given the radical differences in modality of perception and production of sign language, one might expect sign language to differ dramatically in hemispheric asymmetries. But instead our studies have found very strong evidence of highly similar patterns of hemispheric asymmetries in the deaf signing population compared to hearing/speaking individuals.

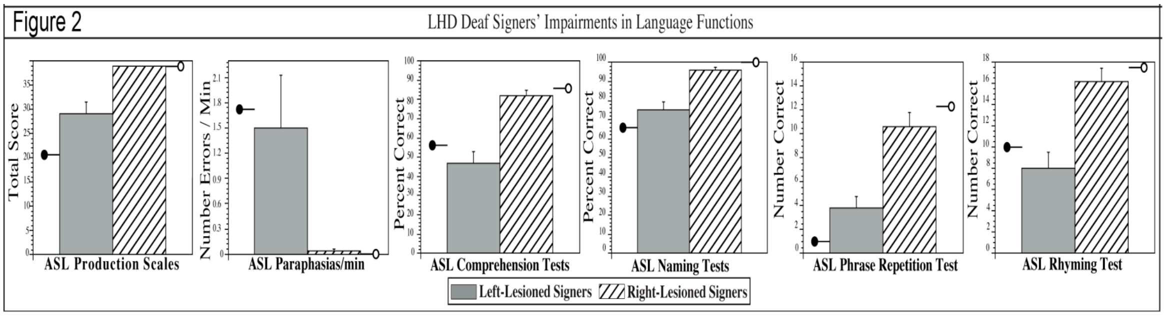
Sublexical-, Lexical-, and Sentence-Level Processes. A variety of sublexical-, lexical-, and sentence-level deficits have been found in individual LHD deaf signers (Poizner, Klima, Bellugi, 1987; Corina, 1998; Hickok, Bellugi, & Klima, 1998a; Hickok, Bellugi, & Klima, 2001). These deficits have been noted both in production, and in comprehension. In production, a range of paraphasic error types have been identified in LHD signers, including "phonemic", morphological, and semantic subtypes, demonstrating the breakdown of these various levels of computation. Some examples of phonemic and paragrammatic paraphasias are shown in Figure 1. Disorders in sign language sentence formation in LHD signers have emerged both in the form of agrammatism and in the form of paragrammatism, showing that sentence-level computations can also be disrupted following LHD in deaf signers (Hickok, Bellugi, & Klima, 1998a; Hickok & Bellugi, 2001). Production errors at all these levels are fairly common in LHD signers, but occur very rarely in RHD signers (Hickok, Bellugi, & Klima, 2002). We have found only one RHD deaf signer who was in fact aphasic, but turned out to be left handed, and with reversed dominance (Clark, Hickok, Love, et al., 1997). As for comprehension, we have documented deficits at the word (i.e., sign) and sentence level (Hickok, Bellugi, Klima, 1998c). At the word level, comprehension deficits have been observed only following LHD, not RHD. At the sentence level, the most severe deficits occur following LHD, but, consistent with findings in the hearing/speaking population, some difficulties in sentence comprehension can be found in RHD signers, particularly as sentence complexity increases (Hickok, Love, & Klima, 2002).

Figure 1 Examples of LHD Sign Errors



Using our ASL-adapted version of the Boston Diagnostic Aphasia Examination (BDAE) (Goodglass & Kaplan, 1983), we have confirmed our case study observations in a group study comparing 13 LHD and 10 RHD signers (Hickok, Bellugi, & Klima, 1998c). LHD signers performed significantly worse than RHD signers on a range of standard language measures, including production, comprehension, naming, and repetition (Figure 2). We have found that these differences between LHD and RHD signers is not a function of sampling error due to group differences in (i) age at test, (ii) onset of deafness, or (iii) age of exposure to ASL (Hickok, Love, & Klima, 2002). This is not to say that these variables have no impact on sign language organization or language ability, because surely they do at some level of detail, only that the dominant factor which predicts performance on these within-sentence linguistic tests is whether the left or right hemisphere is damaged.

Figure 2 LHD Deaf Signers' Impairments in Language Functions



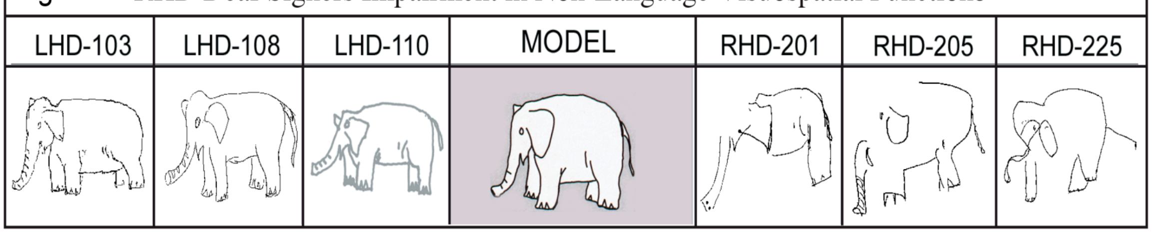
Supra-Sentential (Discourse) Deficits. One linguistic deficit associated with right hemisphere damage in hearing/speaking individuals involves discourse-level processes, e.g., the ability to appropriately link (in production and comprehension) discourse referents across multiple sentences. These deficits manifest as failures to integrate information across sentences, including impairments in understanding jokes, in making inferences, and in adhering to the story-line when producing a narrative. In contrast, phonological and syntactic processes in these hearing/speaking individuals appear to be intact. Using a story narration task given to two deaf RHD signers, we have documented at least two distinct types of discourse deficits (Hickok, Wilson, Clark et al., 1999). The first involves a failure to adhere to the story-line, evidenced by confabulatory or tangential utterances. The second type of deficit involves errors in the use of the spatialized discourse of ASL. Discourse organization in ASL is unique in that discourse referents are established, referred to, and manipulated in a plane of signing space. These results suggest (i) the right hemisphere is involved in discourse processing in ASL, as it is in spoken language, and (ii) there are dissociable subcomponents of discourse processes in ASL.

2. HEMISPHERIC ASYMMETRIES FOR SPATIAL COGNITION

We have found evidence that the lateralization pattern of non-linguistic spatial functions is also similar between deaf and hearing people.

Gross Visuospatial Deficits in RHD Signers. RHD in hearing people often leads to substantial visuospatial deficits evidenced, in the most severe cases, by grossly distorted productions in drawing tasks and block arrangement tasks. Several of the RHD signers we studied presented with similar kinds of gross visuospatial deficits (Hickok, Kirk, & Bellugi, 1998) (Figure 3). Despite sometimes severe non-linguistic visuospatial impairments, none of the RHD signers had aphasia (Bellugi, 2001; Hickok, Bellugi, & Klima,1998b).

Figure 3 RHD Deaf Signers Impairment in Non-Language Visuospatial Functions

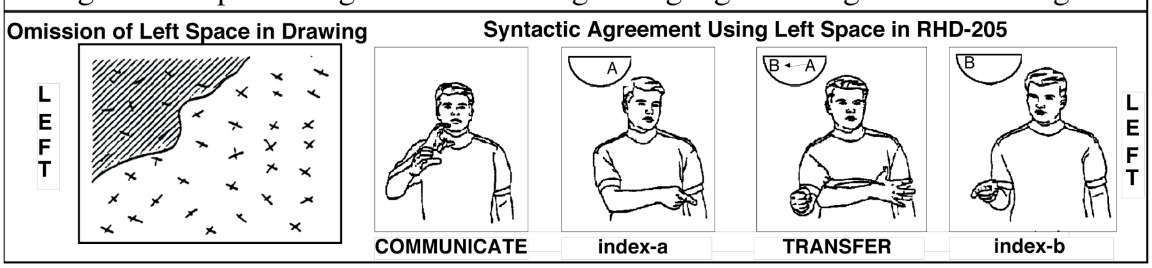


Local/Global Differences. While gross visuospatial deficits may more commonly occur with RHD (both in deaf and hearing populations), it has been reported that some visuospatial deficits can be reliably observed in LHD hearing individuals. When LHD individuals have visuospatial deficits, they typically involve difficulties in attending to and/or reproducing the local-level details of a visuospatial stimulus, while global-configuration aspects are correctly identified/reproduced. RHD hearing individuals tend to show the opposite pattern. Thus, it has been suggested that the left hemisphere is important for local-level visuospatial processes, whereas the right hemisphere is important for global-level processes. We investigated whether a similar asymmetry would be observed in our deaf study population (Hickok, Kirk, & Bellugi, 1998). A group of left or right lesioned deaf signers were asked to reproduce (1) two line drawings (a house and an elephant), and (2) four hierarchical figures, (e.g., the letter 'D' composed of small 'Y's). Drawings were scored separately for the presence of local vs. global features. Consistent with data from hearing patients, the LHD deaf subjects were significantly better at reproducing global-level features, whereas the RHD deaf subjects were significantly better at reproducing local-level features.

Hemispatial Neglect. Hemispatial neglect is a symptom that is strongly associated with RHD in the hearing population. We have noticed a similar association in our deaf study population (Hickok, Kirk, & Bellugi, 1998). Several of the RHD signers presented with significant symptoms of left hemispatial neglect which showed up in drawing tasks, in line cancellation tasks, and in line bisection tasks. Perhaps surprisingly, even severe hemispatial neglect does not seem to interfere substantially with normal sign language communication, either in terms of production or comprehension (Corina, 1998; Hickok & Bellugi, 2001) (Figure 4), except when the patient is asked to communicate information about spatial relations, such as describing the layout of a room (Emmorey, 1998). In one case, for example, an RHD patient with left hemispatial neglect described the layout of furniture in a room using grammatically correct utterances; however, the position of the furniture within the room was incorrectly described, with most of the items "piled up" on the right side of space (Emmorey, 2001).

Figure 4

Neglect for Spatial Cognition but not Sign Language in a Right Lesioned Signer



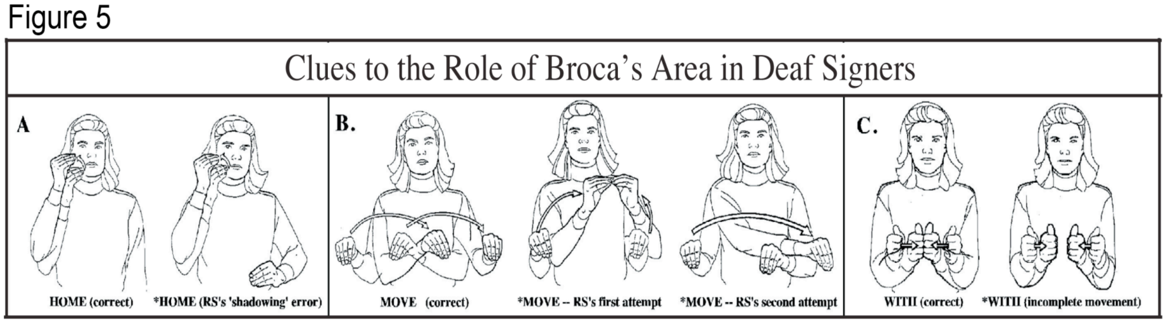
To the extent studied thus far, hemispheric asymmetries for language and spatial cognition in deaf life-long signers is indistinguishable from those found in the hearing/speaking population.

WITHIN HEMISPHERE ORGANIZATION

Functional Aspects: Syndromes and Symptoms. To the extent that the types and patterns of deficits found in sign language aphasia are similar to those found in spoken language aphasia, it would suggest a common functional organization for the two forms of language. There are many commonalities in individual language deficits found; many of the aphasic symptom clusters we have observed in LHD deaf signers fall within the bounds of classical clinical syndromes defined on the basis of hearing aphasics. For example, (i) non-fluent aphasic signers have lesions involving anterior language regions, and (ii) fluent aphasic signers have lesions involving posterior language regions. In addition, the range of common deficit types that have been reported in hearing aphasics have been observed regularly in sign language aphasia. Examples of these include the presence of word (i.e., sign) finding problems in most cases of aphasia, paraphasic errors, and agrammatism, and the tendency for comprehension deficits to be more closely associated with fluent aphasia than with non-fluent aphasia. In addition, the brain lesions producing these patterns of deficits in LHD signers are consistent with clinical-anatomic correlations in hearing people. Based on available evidence to date, it is reasonable to hypothesize that the functional brain organization for signed and spoken language within the left hemisphere may be remarkably similar.

Role of Broca's Area. Broca's area has figured prominently in attempts to determine the anatomy of speech production. We had the opportunity to investigate the role of Broca's area in sign language production through an in-depth case study of LHD-130, a congenitally deaf, native user of ASL, who suffered an ischemic infarct involving the frontal operculum and inferior portion of the primary motor cortex (Hickok & Bellugi, 2001). Acutely, she presented with sign "mutism", consistent with what one might expect in a hearing/speaking individual. Chronically, she had good comprehension, fluent production with occasional sign finding problems, semantic paraphasias, and what appeared to be a deficit involving the ability to control bimanual movements during sign production. That deficit showed up (i) in her tendency on one-handed signs, to "shadow", with her non-dominant hand, sign-articulatory gestures carried out by her dominant (Figure 5a), (ii) in her tendency on two-handed signs, to assimilate the handshape and/or movement of the non-dominant hand with that of the dominant hand (Figure 5b), and (iii) in her occasional failure to complete the movement of a two handed sign when the movement's endpoint involved contact between the two hands (Figure 5c). We were not able to find any evidence of a bimanual control deficit in non-linguistic tasks. Blumstein has suggested that speech production errors in anterior aphasia reflects a breakdown at the phonetic (not phonemic) level caused by a loss of the ability to coordinate independent speech articulators (e.g., larynx, tongue, lips). For a signer, the two hands are independent articulators which are often required to perform independent (i.e., non-symmetric) movements. The deficit observed in LHD-130 may represent the sign analogue of a phonetic-level breakdown. This case suggests that Broca's area plays an important role in sign production.

Figure 5



<u>Neurology of Sign Comprehension.</u> Auditory comprehension deficits in aphasia in hearing/speaking individuals are most closely associated with left temporal lobe damage. This makes intuitive sense given that the temporal lobe contains primary and secondary auditory fields. Because the sensory input of a deaf signer is via the visual system, one might expect that the temporal lobe plays a less important role in sign language comprehension, with more posterior visual-related cortical fields playing a larger role. We investigated the relative role of the left versus right temporal lobe in the comprehension of ASL (Hickok, Love, & Klima, 2002; Hickok, Love, Buchsbaum & Bellugi, 2002). Nineteen life-long signers with unilateral brain lesions (11 LHD, 8 RHD) performed three tasks, an isolated single-sign comprehension task, a sentence-level comprehension task involving one-step commands, and a sentence-level comprehension task involving more complex multi-clause/multi-step commands. Performance was examined in relation to two factors: whether the lesion was in the right or left hemisphere and whether the temporal lobe was involved or not. The LHD group performed significantly worse than the RHD group on all three tasks confirming left hemisphere dominance for sign language comprehension. The group with left temporal lobe involvement was significantly impaired on all tasks, whereas the other three groups performed at better than 95% correct on the single sign and simple sentence comprehension tasks, with performance falling off only on the complex sentence comprehension items. A comparison with previously published data suggests that the degree of difficulty exhibited by the deaf RHD group on the complex sentences is comparable to that observed in hearing RHD subjects. This result suggests that language comprehension depends primarily on the integrity of the left temporal lobe, independent of modality.

FURTHER DISSOCIATIONS

The functional divisions within the neural systems supporting language and other cognitive abilities have been highlighted by several dissociations observed in deaf signers to date.

<u>Dissociations between Linguistic and Non-Linguistic Spatial Abilities.</u> It was noted above that LHD, but not RHD, frequently produces aphasia in deaf signers whereas RHD, but not LHD, frequently produces gross visuospatial deficits. This pattern of deficits constitutes a double dissociation between sublexical-, lexical-, and sentence-level aspects of spatialized linguistic ability on the one hand, and gross non-linguistic spatial cognitive ability on the other (Hickok, Bellugi, & Klima, 1998a; Hickok, Bellugi, & Klima, 1998c). Additional dissociations between sign language abilities and non-linguistic spatial abilities have been demonstrated both <u>within</u> the left hemisphere and <u>within</u> the right hemisphere. Within the left hemisphere we examined the relation between local-level visuospatial deficits evident on a drawing copy task, and several measures of sign language ability, including rate of paraphasias in running sign, single sign comprehension, and sentence-level comprehension (Hickok, Kirk, & Bellugi, 1998). No significant correlations were found between the hit rate for local features in the drawing copy task and any of the sign language performance measures. In fact, cases were identified in which local-level scores were near perfect, yet scores on tests of sign language ability were among the worst in the sample. This suggests that aphasic deficits cannot be reduced to a more general deficit in local-level visuospatial processing. Within the right hemisphere, two case studies have provided evidence that the ability to use the spatialized referential system in ASL discourse does not depend substantially on non-linguistic visuospatial abilities of the right hemisphere (Hickok, Wilson, Clark, et al., 1999). Case RHD-221 had severe visuospatial deficits following a large right perisylvian stroke, yet was not impaired in his ability to set up and utilize spatial loci for referential purposes. Case RHD-207, showed the reverse pattern. Her performance on standard visuospatial tasks was quite good, yet she had difficulty with spatialized aspects of ASL discourse. This finding hints at the possibility that there are non-identical neural systems within the right hemisphere supporting spatialized discourse functions versus non-linguistic spatial abilities.

Dissociations within Spatialized Language Systems. In addition to using space to encode grammatical and discourse information, ASL uses space in an iconic fashion to represent spatial information directly, as, for example, in describing the layout of objects in room. It is worth making the distinction clear between the grammatical use of space in ASL, to encode phonological, morphological, syntactic information as described previously, and the spatial use of space to express spatial relations. Spoken language communicates spatial information through the use of prepositions and spatial description words as in, "The cup is *near* the *left*, *front* corner of table *behind* the fork." Note that the grammaticallity structure of such a sentence is independent of how accurate the spatial information is. So while it may or may not be the case that the cup is behind the fork, it certainly is the case that the sentence itself follows the rules of the grammatical structure of English (as opposed to "cup near corner left front table."). In ASL, instead of using lexical means to communicate spatial information, the location of objects relative to one another is physically mapped out in (signing) space (Emmorey, 2001). As in the spoken language example, the grammaticallity structure of a signed sentence is independent of the truth value of the content.

We wondered whether the grammatical use of space could be dissociated from the spatial use of space even when these types of information are expressed in the same channel. To investigate this question, we tested the performance of two deaf, native signers -- one with left hemisphere damage and one with right hemisphere damage -- on comprehension tasks involving the use of space, within ASL, to represent grammatical versus spatial information (Hickok & Bellugi, 2001). In the grammatical task, we presented signed sentences similar to "the cat chased the dog" in which the grammatical subject and object of the verb was indicated spatially; the task was to select a picture that matched the meaning of the sentence. In the spatial task, we presented a signed description of the layout of furniture in a room followed by a picture that either matched that description or did not; the task was to indicate whether the picture matched the description. We found a double dissociation: LHD-130 was impaired on tasks involving the use of space for encoding grammatical information (64% correct), but performed well on tasks involving the use of space to encode spatial information iconically (100% correct). The RHD-216 showed the reverse pattern (89% and 50%, respectively). These data suggest that the neural organization for language and spatial cognition are driven by the type of representation that is ultimately constructed from the signal (grammatical vs. spatial), rather than by the physical properties of the signal itself.

Dissociation between Linguistic and Affective Facial Expression in ASL. So far, our investigations of brain organization for sign language have focused on manual signs. However, there is another layer of structure of sign language that provides special clues to the basis of hemispheric specialization; namely, facial expressions. For ASL, facial expressions function in two distinct ways: (i) specific facial expressions have arisen as a part of the grammar, co-occurring with manual signs and are used to mark various syntactic structures such as relative clauses, topics, etc.; and (ii) facial expressions can convey affective information, just as facial expressions do with hearing nonsigners. In addition, facial expression and body postures can function to identify role shifts, an issue we will return to. Our studies over two decades assessed the effects of right- and left-hemisphere lesions on linguistic and affective facial expression in ASL. We found a dissociation between some RHD and LHD signers in terms of production of the two different functions of facial expression: linguistic and affective. The LHD subjects showed full use of affective facial expression, but with frequent omissions of linguistic facial expression where required. In contrast, the RHD subjects tended to produce linguistic facial expressions where required but exhibited less affective signals. These are important findings since presumably one and the same muscular system is involved; the findings show that linguistic and affective facial signals in ASL may be differentially lateralized for deaf signers (Corina, Bellugi, & Reilly, 1999).

Dissociation between Aphasia and Apraxia. The data discussed thus far suggests that sign language deficits cannot be reduced fully to domain-general spatial cognitive deficits. To what extent can sign language deficits be reduced to domain-general motor skills? In order to address this question, we administered an abbreviated version of Kimura's Movement Copy Test (Kimura, 1993) to 11 LHD subjects. This task involved copying non-representational manual movements using the arm ipsilateral to the lesion. We did find varying degrees of disruption in the ability to perform this task, consistent with the tendency for hearing LHD patients; however, scores did not correlate significantly with measures of sign production during connected sign, including number of paraphasias per minute, number of paraphasias when corrected for number of signs produced, or fluency as defined in the Boston Diagnostic Aphasia Examination phrase length scale (Hickok, Bellugi & Klima, 1998b). Further, on each of the language measures, subjects could be identified who produced similar scores in terms of their sign production yet differed substantially in their apraxia score, indicating the dissociability between the two domains. While it is difficult to rule out fully the existence of a significant correlation between these variables because of the relatively small sample size, these data suggest that there is a significant amount of variability in at least some aspects of sign language disruption that cannot be accounted for solely by a disruption of voluntary motor control.

Dissociations between Sign and Gesture. Evidence supporting the view that deficits in sign language are qualitatively different from deficits in the ability to produce and understand pantomimic gesture comes from a case study of a LHD signer (Corina, 1998; Emmorey, 2002). Following an ischemic infarct involving both anterior and posterior perisylvian regions, LHD-108 became aphasic for sign language. His comprehension was poor and his sign production was characterized by frequent paraphasias, reduced grammatical structure, and a tendency to substitute pantomime for ASL signs -- a tendency not present prior to his stroke. These pantomimic gestures were used even in cases in which the gesture involved similar or more elaborate sequences of movements arguing against a complexity-based explanation of his performance. LHD-108 showed a similar dissociation in his comprehension of signs versus pantomime where he had more trouble matching a sign to a picture than matching a pantomimed gesture to picture. This case makes the point that disruptions in sign language ability are not merely the result of more general disruptions in the ability to communicate through symbolic gesture. Since this initial report, we have seen several additional patients who show a similar tendency to use gesture in place of lexical signs.

EVIDENCE FROM FUNCTIONAL NEURO-IMAGING

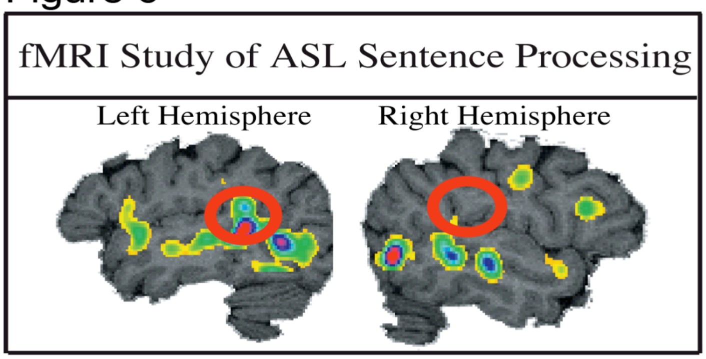
Lesion evidence has indicated clearly that hemispheric asymmetries for signed and spoken language are similar, and has provided some indication that the within hemisphere organization of signed language is also similar to that of spoken language. But the spatial resolution of the lesion method is poor, particularly in a rare population, limiting the amount of information one can derive from lesion studies alone. The development of new functional imaging methods has allowed investigators to take a closer look at the within hemisphere organization of sign language. The first studies examined the role of Broca's area in sign production. Further studies have documented that Broca's area is, in fact, activated during sign production, consistent with lesion evidence (Hickok & Bellugi, 2001).

Neural Systems Underlying ASL Sentence Processing. More recent work has examined regions involved in sign language comprehension. We conducted a study in which deaf native signers viewed short sentences in ASL in a passive viewing paradigm. We found bilateral activation in ventral occipital-temporal cortex and the STS similar to the results of Neville, et al. (Neville, et al., 1998). Parietal lobe regions were not reliably activated in our study (or the Neville et al. study), nor were auditory cortices in the supratemporal plane (the dorsal surface of the temporal lobe which contains primary and secondary auditory cortices). This result shows that many traditional language processing areas within the left hemisphere are activated during sign comprehension, including portions of Wernicke's area. Some authors have emphasized the bilateral activation pattern in the Neville et al. study, and used this observation to argue that ASL may be more bilaterally organized than spoken language (Neville, et al., 1998). The lesion evidence we have gathered, however, clearly indicates a similar pattern of hemispheric asymmetries for signed and spoken language, including comprehension ability (Hickok, Bellugi, & Klima, 1998b). Furthermore, in our fMRI study, we observed a hemispheric asymmetry (left > right) in 4 out of the 5 subjects in the left posterior planum temporale -- a result not reported previously. Figure 6 shows single subject data showing activation in superior temporal cortex and portions of frontal cortext. Note no posterior parietal activation and the hemispheric asymmetry in the planum temporale region (left>right). This region is also strongly activated in hearing subjects listening to speech stimuli. (Hickok, Love, Buchsbaum, & Bellugi, 2002).

We have recently followed up on the observed activation in the left planum temporale region during sign perception/comprehension. FMRI data from studies carried out by

Hickok et al have shown that this same region shows sensory-motor response properties in the speech domain: i.e., it responds both during the speech perception, and during (covert) speech production. We borrow a paradigm from these studies in hearing subjects, and asked native deaf participants to view sets of non-signs and then covertly rehearse them for several seconds. The sensory and "motor" phases of the trial were separated out using multiple regression techniques. We wished to address two questions, (i) would this posterior planum area that shows sensory-motor responses with speech stimuli in hearing subjects, also show sensory-motor responses to sign stimuli in deaf subjects, and (ii) would posterior parietal regions known to be involved in visuo-motor integration (e.g., visually guided reaching) show sensory-motor responses in the deaf subjects (it does NOT in the hearing subjects with speech stimuli)? The answer to these questions, is "yes" in both cases. We found robust visuo-motor activations in the posterior planum area on the left not the right, as well as in parietal regions bilaterally. Since this paradigm is quite similar to verbal working memory paradigms these activations also probably outline systems which are important for the short term retention of sign information. Several studies are planned under the renewal to further explore the implications of these findings for both sensory-motor integration processes and verbal working memory in sign language.

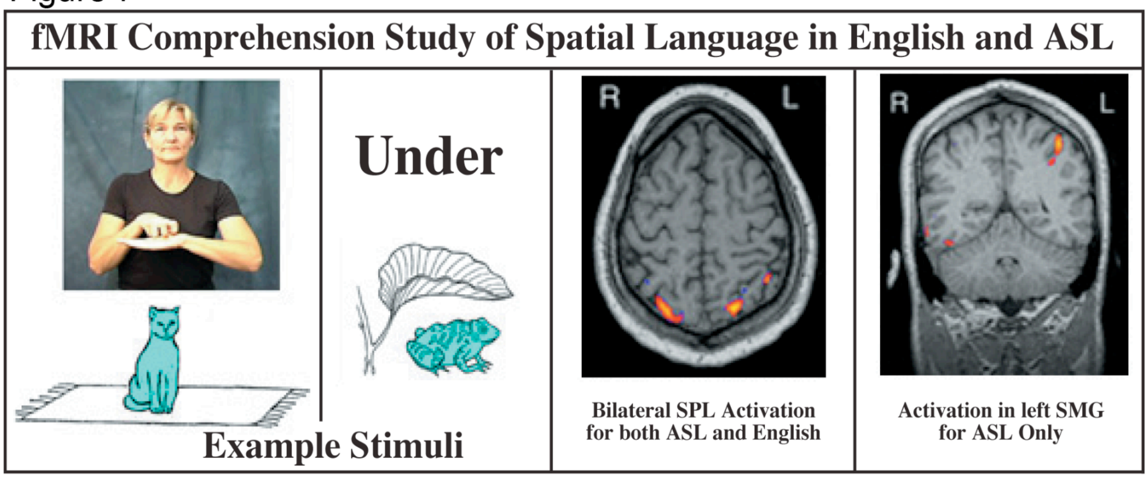
Figure 6



<u>Neural Systems Underlying Language about Space.</u> Signed languages differ dramatically from spoken languages with respect to how spatial information is encoded linguistically. Rather than specifying spatial relations with a closed-class set of prepositions, signed languages encode spatial relationships using space itself. Specifically, signers produce spatial descriptions using *classifier constructions* in which classifier signs are placed within three dimensional signing space to represent the spatial relationships among objects in the real (or imagined) world. Such spatialization of linguistic encoding has ramifications for the neural systems that underlie spatial language. Our lesion studies indicate that damage to the right hemisphere can impair the production and comprehension of ASL spatial descriptions. However, the lesions producing these impairments were quite varied, providing few clues as to which right hemisphere structures are critically involved. Evidence from separately funded studies of sign language <u>production</u> using Positron Emission Tomography (PET) indicates a critical role for right parietal cortices (both posterior superior parietal cortex and the supramarginal gyrus) in the production of spatial language (Emmorey, Damasio, McCullough, et al., 2002). We have recently conducted a comprehension study of spatial language in English (hearing participants) and in ASL (deaf participants) using fMRI.

English speakers were presented with pictures labeled with a preposition, and ASL signers were presented with pictures labeled with a locative classifier construction (Figure 7). The subjects' task was to determine whether the linguistic description

Figure 7



matched the spatial relation depicted in the picture (the figure object was always tinted blue). The baseline task for English speakers consisted of "visual noise" (scrambled pictures) with letter strings matched for length with the prepositions. Similarly, the ASL baseline consisted of scrambled pictures and an image of a signer (with hands down) above the picture. Subjects were instructed to press "yes" and "no" response buttons alternatively during the baseline condition. The baseline conditions control for motoric response and for low-level visual processing of the line drawings and face processing for the ASL stimuli.

Preliminary results from six subjects indicate that comprehension of both English prepositions and ASL locative classifier constructions engages posterior superior parietal lobule (SPL) bilaterally. Activation in SPL is likely to reflect visuospatial processing required to determine whether the spatial relation shown in the picture matches the linguistic label. In addition, activation was observed in left perisylvian language cortices for both English and ASL (specifically, left inferior frontal gyrus and superior temporal cortex). Interestingly, the primary difference between the two languages (and subject groups) was activation in left inferior parietal lobule (supramarginal gyrus) for the ASL signers. Such activation may reflect a unique role for left inferior parietal cortex in the comprehension of ASL spatial descriptions. Data from fMRI studies provide evidence for what structures may be involved in comprehension of spatial language in ASL, while data from the lesion studies indicates what structures are essential.

SUMMARY

We have found that despite the radical surface differences between spoken and signed languages, the neural organization of signed language is remarkably similar to that of spoken language. Left perisylvian damage in deaf signers produces sign language deficits much like those found in hearing individuals with left perisylvian damage. Further, functional imaging and lesion evidence suggests that Broca's area participates in sign language production and that the lateral temporal lobe is a site critical for sign language comprehension. Right hemisphere damage in deaf signers does not produce marked aphasic deficits, but has been associated with discourse-level sign language deficits. Language abilities in deaf signers appear to be dissociable from a variety of non-linguistic visuospatial abilities, from non-linguistic symbolic-gestural abilities, and from non-symbolic praxic abilities. The sensory interface system seems to constitute the major difference between the neural organization of signed versus spoken language: speech perception appears to rely on systems in the dorsal superior temporal gyrus, sign perception does not appear to activate this region. We hypothesize that sign analogue of speech perception is carried out in unimodal visual cortex, whereas higher-level (i.e., supramodal) language processes (lexical, morphological, syntactic) are carried out in canonical left perisylvian language regions. Thus, despite a prior expectations, radical differences in the peripheral sensory and motor interface systems between signed and spoken language appear to have little effect on the neural organization of core aspects of the linguistic system.

Our goal is to elucidate the biological bases of human language. We approach this issue through the study of the neural organization of ASL, a language displaying the complex linguistic structure of spoken languages, which uses space at multiple linguistic levels and encodes much of its linguistic information spatially. The study of the neurobiology of ASL, by allowing us to separate out modality-dependent from modality-*in*dependent contributions to neural organization for language, provides a direct window on brain organization for language itself.

Our studies are providing striking evidence that language is subserved by neural systems whose neuro*functional* organization is quite independent of the modality in which language is cast — following focal brain damage, similar types of primary language disturbances (aphasias) occur in both deaf signers and hearing non-signers. The neuro*anatomical* organization is also largely independent of modality — sign aphasia occurs following damage to the left but not the right hemisphere of the brain for *both* deaf signers and hearing non-signers. Our studies are uncovering evidence that there are some differences in the neuroanatomical organization of signed vs. spoken languages *within* the left hemisphere. These findings may help tease apart central and peripheral aspects of the neural organization of language. In addition, new understanding of *right* hemisphere functional and neuroanatomical organization is emerging from our studies involving the uses of space in ASL to express discourse functions and to directly encode spatial relations. We are discovering dissociable functions within the right hemisphere that reflect the spatialized nature of ASL discourse, and our studies are revealing the critical role of the right hemisphere in interpreting spatial relations encoded directly in the signing space.

Our findings have a major impact on scientific thinking regarding the nature of human language. This research demonstrates the extent and limits of neural plasticity in the developing brain. Mapping the biological organization of language in general, and of signed languages in particular, is central to the concerns of cognitive neuroscience. These studies will directly benefit clinicians, caregivers, and educators by providing crucial information about deaf individuals with brain damage, as well as opening the door to deeper investigations of the underpinnings of language and language disorders.

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