What’s right about the neural organization of sign language? 
A perspective on recent neuroimaging results

Gregory Hickok, Ursula Bellugi and Edward S. Klima

What is the basis for the neural organization of language? Are posterior language systems (e.g. Wernicke’s area) situated in auditory association cortex simply because linguistic information is channeled through the auditory system during development? Are anterior language systems (e.g. Broca’s area) situated in inferior premotor/prefrontal cortex simply because it’s the inferior portion of motor cortex that controls the speech articulators? Is the left hemisphere dominant for language simply because that hemisphere happens to be dominant for processing sequentially organized information that changes rapidly in time (a prominent characteristic of acoustic-speech information), or because that hemisphere happens to be dominant for the control of purposeful movement? Or is it possible that language is organized the way it is because the systems in question are somehow biased towards processing linguistic information, independent of modality.

Evidence from sign language
Sign language provides a unique perspective on these questions. Because signed and spoken languages share linguistic representational structure, but differ radically with respect to their surface sensory and motor forms, a comparison of the neurobiology of the two systems can lead to a better understanding of the brain organization for linguistic processing with modality-specific contributions factored out. There is now a relatively large body of evidence relevant to this issue. Neuropsychological studies have uniformly confirmed a dominant role for the left hemisphere in sign language understanding and production in deaf signers. A number of case studies and one relatively large-scale group study of unilateral brain lesioned signers have shown that left hemisphere damage often produces aphasia for sign language whereas right hemisphere damage does not. The differential effects of left versus right brain damage in the deaf signing population can be seen from Fig. 1. This effect holds even when one controls for variables such as age of onset of deafness, age of exposure to sign language, and length of deafness.

![Fig. 1 Group data showing the effects of left versus right-hemisphere damage on American Sign Language (ASL) ability in deaf life-long signers. Note that, relative to normal subjects (A) and patients with right-hemisphere damage (n = 7) (B), left-hemisphere damaged patients (n = 10) (C) present with a range of deficits in ASL ability. The 7-point rating scales for each measure of performance are as follows: Melodic line (‘absent’ (1) through ‘limited to short, stereotypical phrases’ (4) to ‘runs through entire sequence’ (7)); Phrase length (‘single signs’ (1) through ‘short strings of signs’ (4) to ‘normal length’ (7)); Articulatory agility (‘always impaired’ (1) through ‘normal only in familiar signs and phrases’ (4) to ‘never impaired’ (7)); Grammatical form (‘none’ (1) through ‘limited to simple declaratives and stereotypes’ (4) to ‘normal range’ (7)); Paraphasia in running sign (‘always present’ (1) through ‘once per minute of conversation’ (4) to ‘absent’ (7)); Sign finding (‘fluency without information’ (1) through ‘information proportional to fluency’ (4, normal condition) to ‘exclusively content signs’ (7)); Sign comprehension, from ‘absent’ to ‘normal’)]
language, and age at testing). Further, sign language deficits have been shown to dissociate from deficits of voluntary motor control (gestural ability), and various types of non-linguistic spatial ability. Several additional approaches lend support to this contention. For example, dual-task studies and studies using lateralized visual field presentation of sign stimuli in normal deaf signers have corroborated language lateralization conclusions based on lesion studies. And a case report of an intracerebral amobarbital procedure performed on a deaf signer has confirmed that the left but not the right hemisphere is sufficient to support sign language ability. Finally, there are functional imaging data demonstrating left hemisphere dominance in sign language production. Both an FMRI study of the production of American Sign Language (ASL) words, and a PET study of the production of ASL sentences have shown activation of Broca's area. Together, these data provide compelling support for the view that the lateralization of language to the left hemisphere is modality independent.

Right on in sign language? Against this backdrop, a more recent functional neuroimaging study of sign language perception in a group of normal deaf signers and hearing bilingual signers has led some investigators to reconsider the role of the right hemisphere in processing sign language. The evidence in question comes from an FMRI study by Neville and colleagues which looked at the neural organization of sign language perception in deaf and bilingual signers. They found that native signers (both deaf and hearing) showed robust activation of perisylvian regions of the left and the right hemispheres in response to viewing a signer producing ASL sentences, whereas hearing subjects showed only left hemisphere activation upon reading printed English sentences (Fig. 2). To similar areas in the left hemisphere were activated in response to signed and spoken language, but only ASL activated the right hemisphere. Therefore, Neville and colleagues suggest that the activation of right hemisphere areas when hearing and deaf native signers process sentences in ASL, but not when native speakers process English, implies that the specific nature and structure of ASL results in the recruitment of the right hemisphere into the language system.

Right on in spoken language? We now discuss these points in turn. Potential confounds. The observed differences in activation produced by ASL and English sentences in the Neville et al. study could have been produced by any number of factors that either were, or may have been present in the ASL stimuli but were certainly absent in the English stimuli. These include, for example, an aspect of language associated with right perisylvian regions, emotional facial expressions on the signer, and meaningful non-linguistic gestures (which occur with signed as well as spoken language) – in short, all of the ‘extra-grammatical’ communicative aspects of language use. Evidence that factors such as these could have contributed to the observed differences in Neville et al.'s study comes from lesion studies showing extra-grammatical deficits in right-lesioned deaf signers, and from functional imaging experiments showing bilateral activation in hearing subjects listening to spoken language. A more appropriate, indeed critical, comparison condition then, would be to have hearing subjects listen to and view an individual speaking English sentences, as deaf subjects viewed an individual signing ASL.

In fact, there has been one published study that made this comparison. Siderofsky et al. measured regional cerebral blood flow (rCBF) using the Xenon method in a population of hearing signers of deaf parents (i.e., they have native proficiency in both a sign and spoken language) while they (1) viewed signed versus spoken language sentences, (2) viewed and listened to a speaker producing spoken language sentences, (3) just listened to spoken language sentences. Compared to a resting condition, both sign language and spoken language produced increases in rCBF in posterior temporal lobe regions bilaterally. A direct comparison between viewing signed sentences and listening to spoken sentences showed greater rCBF in posterior temporal regions for sign language perception, whereas, when sign language perception was compared to viewing and listening to a speaker producing spoken language sentences, no significant differences were observed. While the sensitivity and spatial resolution of the Xenon method is inferior to that of FMRI, the results of this study suggest that the English stimulus is inferior to that of ASL in convincing the viewer that viewing the individual is inferior to that of producing the language (whether spoken or sign) can make a difference in the brain areas involved. A similar control experiment needs to be conducted using FMRI before any conclusions are reached regarding possible differences in the neural organization of signed and spoken language.
actually be consistent with lesion data concerning the lateralization of auditory language processing. For example, Goodglass (1981) observed that the left hemisphere of the basic language operations, auditory language processing is the one which is least an exclusively left-hemisphere prerogative (p. 48). More to the point, a study of the sentence comprehension abilities of left and right lesioned hearing/speaking patients (32) found that while left hemisphere damaged patients performed worse than right hemisphere damaged patients, both groups performed significantly worse than normal controls. Right hemisphere patients (like the left hemisphere patients) also showed an effect of syntactic complexity with more complicated sentences yielding poorer performance. Captain et al. state: ‘The results of this study show that sentence comprehension is affected by lesions in both the left and right hemisphere, more so by the former...’

They also raise the question of a ‘possible contribution of the right hemisphere to [syntactic] processing’ (Ref. 22, p. 94).

The point is that lateralization of function is rarely absolute. This is true of auditory language processing, and is probably true of sign language processing as well. It would not be surprising, then, if the right hemisphere were shown to play some kind of a role in sign language processing. In fact, the similarity of functional imaging techniques may be bringing us closer to picking up these subtle differences.

The real surprise in the Neville et al. study, in our view, is the similarity between the regions activated within the left hemisphere of deaf individuals compared with those activated by spoken language (written or auditory) in hearing individuals. Despite its insular nature, classic left-hemisphere language areas appear to be involved in processing sign language. This is a non-intuitive result. Why are canonical auditory-related structures involved in processing sign language? Why not visual-related cortices? Why is Broca’s area, which is consistently situated just anterior to that portion of the motor cortex controlling speech-related muscle movements, activated in sign language processing? Why isn’t the functional equivalent of Broca’s area shifted more superiority in deaf signers so that it’s aligned with motor cortex controlling the hand and arm muscles?

Further, some authors have speculated that the left parietal lobe may be more involved in processing sign language than that region is in processing spoken language because of the particular role of spatial and visuo-motor functions; yet it showed no significant activations. Apparently traditional left parietal mechanisms are involved in processing not just speech, but language, defined more abstractly, lesion data concerning the left hemisphere organization of ASL support this view (32).

A possible within-hemisphere difference

To summarize the argument so far, our main points are (1) that the vast majority of behavioral, neuropsychological, and functional imaging data support the hypothesis that the left hemisphere is dominant for lexical and grammatical aspects of sign language perception and production, (2) that because of potential design confounds, the Neville et al. study does not present any serious challenge to existing claims concerning the lateralization of sign language, and (3) that there is evidence from both lesion and functional imaging data which suggests that the within-hemisphere organization of signed and spoken language is in many respects the same – but not in all respects.

One difference (which has been overlooked thus far) in the brain regions that were activated in the processing of ASL stimuli compared with those that are activated in the processing of auditorily presented spoken language stimuli concerns the supratemporal plane structures. This region is uniformly activated in hearing subjects listening to spoken language (41,42) but was not activated in deaf subjects watching ASL sentences in the Neville et al. study, nor was it activated in an fMRI study of single-sign perception in a native deaf signer (23).

One potential explanation for this is that supratemporal plane structures are involved in processing non-linguistic auditory information (32) because these are not language processing systems, perception of ASL would not be expected to activate these areas; speech stimuli on the other hand, would produce activation in supratemporal plane as a result of some type of acoustic response. Another possibility, however, is that the supratemporal plane contains systems directly and critically involved in the perception of speech (that is, extracting linguistic information from an auditory signal), as some authors have suggested (Ref. 27 and D. Poeppel, PhD thesis, MIT, 1995). This hypothesis could explain the presence of supratemporal activation in auditory language perception and its absence in sign language perception. It also predicts that there should be some processing system outside of canonical language areas involved in the extraction of sign information from the visual input. On this view, there are both modality dependent and modality independent components to the neural organization of language perception. Modality dependent components are those involved in extracting linguistic information from the sensory input, modality independent components are those involved in operating on higher-level linguistic representations. Based on available data, it’s possible that supratemporal plane structures are part of a modality dependent system involved in speech perception, whereas lateral temporal lobe structures are part of a modality independent system involved in higher-level linguistic operations.

But all of this discussion hasn’t really answered the question posed at the outset; that is, what is driving the neural organization of language? Well, we don’t know so far. In fact, the data reviewed above render this problem a bit more puzzling (and thus perhaps more interesting). What we do know is that modality-specific factors aren’t the whole story. Speculation for the possibility of speech perception, the neural organization of language appears to be largely independent of the modalities through which it is perceived and produced. But notice that this conclusion rules out the most intuitive and probably the oldest answer to the above question, namely that language systems are really just dynamically organized subsystems of the particular sensory and motor channels through which language is used. Instead, the answer will have to be couched in terms that can generalize over modality. Whether such an account will ultimately appeal to genetically constrained domain-specific regional specializations or to some complex interaction of domain-general processing systems (or both) remains to be seen. Provocative issues indeed.
procedure performed for a deaf patient with a C1 lesion. Neuroradiol. 33, 11–15.

Response from Corina, Neville and Bavelier

T he commentary by Hickok, Bellugi and Klima raises several issues regarding our recently published functional neuroimaging reported only of native deaf and hearing signers processing American Sign Language (ASL) and English. In this paper we presented the first and most detailed assessment of ASL and English comprehension in native signers using the highest field-strength functional neuroimaging techniques currently available. Our findings are provocative, for, in addition to showing the contributions of classical left-hemisphere perisylvian language areas in sign language comprehension in na- tive signers, they also reveal consider- able right-hemisphere (RH) activation. This RH activity was not predicted by studies of aphasia in deaf signers, which have argued for an exclusive role of the left hemisphere in ASL processing. We maintain that this RH activity reflects language processing requirements of a sign language which are not observed in the process- ing of written English.

The Hickok et al. critique raises two main issues about this study: (1) What is the source of the RH activation? (2) How do the activation patterns of the left hemisphere help address issues related to the neurobiology of linguistic processing? The issues of left-hemisphere processing are complex and cannot be adequately addressed in this brief forum. Rather, we focus here on a discussion of the RH involvement observed in our study.

To determine the organization of the left-hemisphere Broca’s area homol- ogous and dorsolateral prefrontal cortex. This suggests that specialization of these frontal areas for language processing may be dependent upon different in sensory input at forma- tion is independent of the form of the lan- guage. In addition, the extensive activi- tion of the right hemisphere reflects that the specific processing require- ments of a language also, in part, determine the organization of the language systems of the brain.

We therefore agree with Hickok et al. with respect to the importance of right-hemisphere structures in the medi- cation of signed languages. We differ, however, with respect to the relative importance of the extensive RH activa- tion observed in the fMRI study of ASL processing. It is important to note that several groups using PET and fMRI techniques have reported RH activa- tion of temporal and frontal areas in response to spoken language process- ing tasks (see Box 1). Thus, findings of RH activity in language studies should not come as a complete surprise to Hickok et al.

However, we do believe that the RH activity observed when native signers processed ASL is qualitatively different. Several observations support this claim. First, in these spoken lan- guage experiments the RH activity is never as functionally robust as the left hemisphere activity. In our study, the RH activation of native signers in the ASL condition was as robust as that ob- served for the left hemisphere. Second, the RH regions identified in spoken language studies tend to be restricted to small portions of the temporal lobe and, less frequently to the frontal lobe. The RH activation observed in the signers processing ASL is extensive, and extends to frontal, temporal and parietal sites. Finally, it is particularly interesting that only in deaf native signers do we find reliable activity of a

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