

What's right about the neural organization of sign language?

A perspective on recent neuroimaging results

Gregory Hickok, Ursula Bellugi and Edward S. Klima

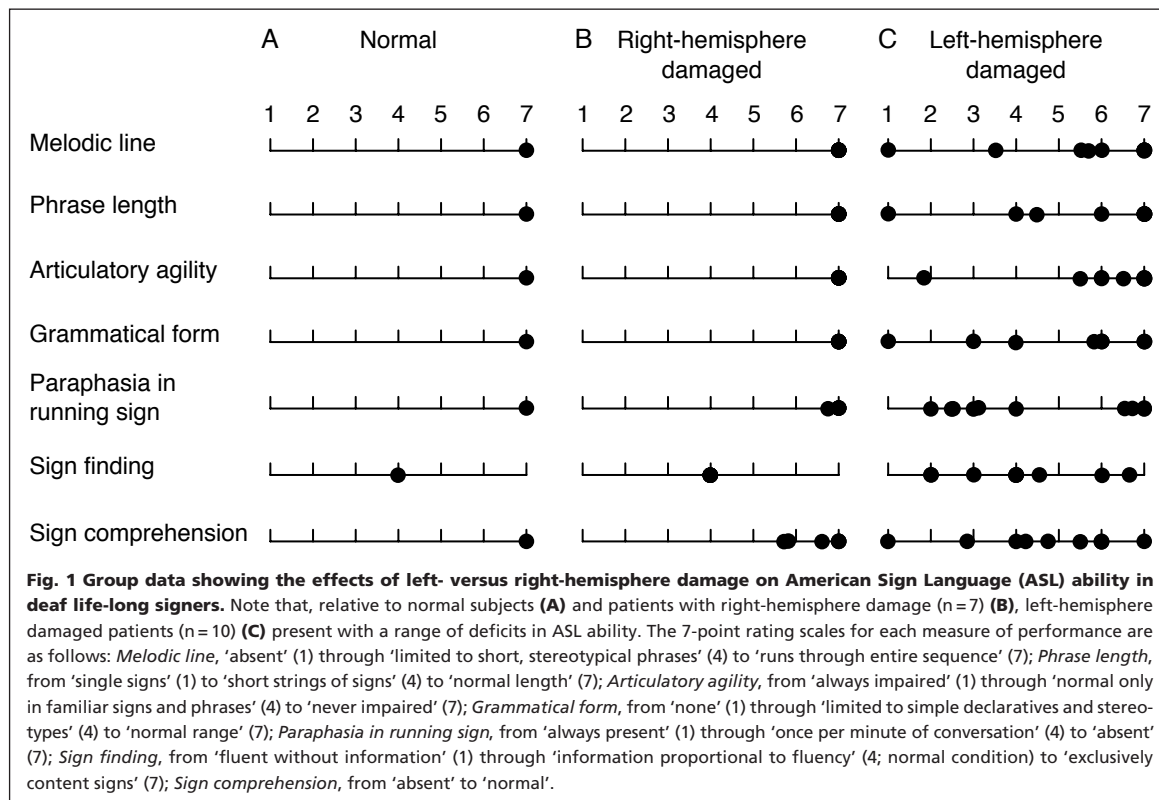
What is the basis for the neural organization of language? Are posterior language systems (e.g. Wernicke's area) situated in auditory association cortex simply because linguistic information is channeled through the auditory system during development? Are anterior language systems (e.g. Broca's area) 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

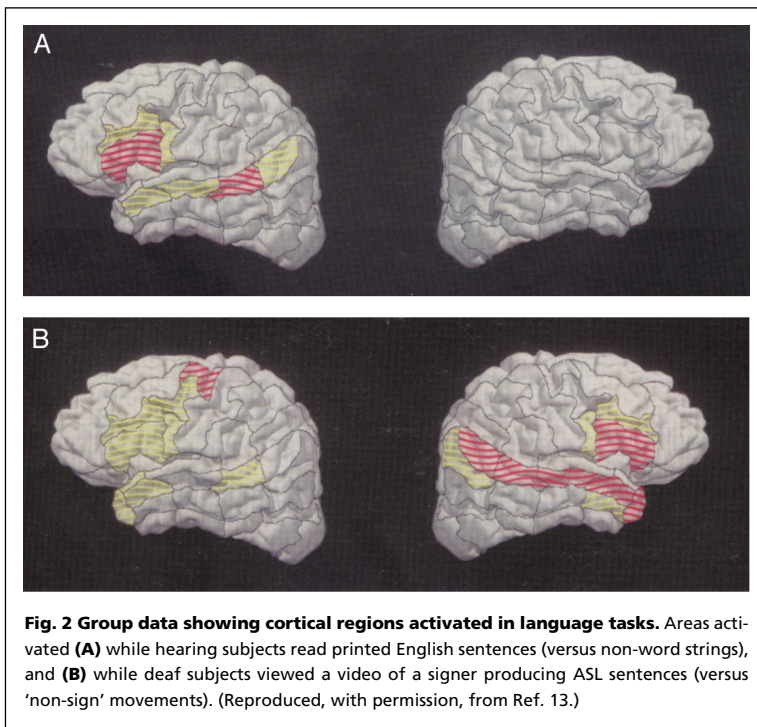
contributions factored out. There is now a relatively large body of evidence relevant to this issue. Neuropsychological studies have uniformly confirmed a dominant role for the left hemisphere in sign language understanding and production in deaf signers^{1,2}. A number of case studies^{2,3} and one relatively large-scale group study⁴ 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



G. Hickok is at the Department of Cognitive Sciences, University of California, Irvine, CA 92697, USA.

tel: +1 949 824 1409
fax: +1 949 824 2307
e-mail: gshickok@uci.edu

U. Bellugi and E.S. Klima are at the Laboratory for Cognitive Neuroscience, Salk Institute for Biological Studies, La Jolla, CA 92037, USA.



language, and age at testing⁴. Further, sign language deficits have been shown to dissociate from deficits of voluntary motor control^{4,5}, gestural ability⁶, and various types of non-linguistic spatial ability^{1,3,4,7}.

Several additional approaches lend support to this contention. For example, dual-task studies⁸ and studies using lateralized visual field presentation of sign stimuli⁹ in normal deaf signers have corroborated language lateralization conclusions based on lesion studies. And a case report of an intracarotid amobarbital procedure performed on a deaf signer has confirmed that the left but not the right hemisphere is sufficient to support sign language ability¹⁰. 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) words¹¹, and a PET study of the production of ASL sentences¹² 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 colleagues¹³ 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). So similar areas in the left hemisphere were activated in response to signed and spoken language, but only ASL activated the right hemisphere. Why the difference? Neville et al.¹³ 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' (p. 928). Paulesu and Mehler¹⁴ in a recent review of these data entitled 'Right on in sign language' state that this study 'raises some provocative issues about the cerebral organization of language' and go on to consider the possibility 'that ASL is implemented in such a unique sensory modality that its cortical representation is also unique' (p. 234).

We agree fully with Paulesu and Mehler that the Neville et al. study raises some provocative issues, but we disagree about which aspects of the results are controversial. It is our view that interpretation of the differences in these functional imaging activations produced by signed versus spoken language is premature; the appropriate control experiments simply have not yet been carried out, and there is much contradictory data in the literature, as the above authors point out. The most provocative aspect of Neville et al.'s study in our view is, rather, the high degree of similarity in the left hemisphere regions activated by ASL and English sentences. 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 prosody (an aspect of language associated with right perisylvian regions¹⁵), 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^{5,7}, and from functional imaging experiments showing bilateral activation in hearing subjects listening to spoken language^{16–19}. A more appropriate, indeed critical, comparison condition then, would be to have hearing subjects listen to and view an individual speaking English sentences, just as deaf subjects viewed an individual signing ASL.

In fact, there has been one published study that made this comparison. Söderfeldt et al.²⁰ measured regional cerebral blood flow (rCBF) using ¹³³Xenon in a population of hearing signers of deaf parents (i.e. they have native proficiency in both a signed and spoken language) while they (1) viewed signed 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 (only) to spoken sentences showed greater rCBF in posterior temporal regions for sign language perception. However, when sign language perception was compared to viewing and listening to a speaker produce spoken language sentences, no significant differences were observed. While the sensitivity and spatial resolution of the ¹³³Xenon method is inferior to that of fMRI, the results of this study suggest that viewing the individual who is producing language (whether speech 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.

Right on in spoken language?

We have suggested that the design of the Neville et al. study may not have been suitable for identifying lateralized language systems in deaf signers. Now we would like to make the point that a finding of a role for the right hemisphere in sign language processing may

actually be consistent with lesion data concerning the lateralization of auditory language processing. For example, Goodglass²¹ writes: 'Of the basic language operations, auditory language processing is the one which is least an exclusively left-hemisphere prerogative' (p. 43). More to the point, a study of the sentence comprehension abilities of left and right lesioned hearing/speaking patients²² 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. Caplan *et al.* state: 'The results of this study show that sentence comprehension is affected by lesions in both the left and the 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. 944).

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. The sensitivity of functional imaging techniques may be better suited to picking up these subtle differences.

The real surprise

The real surprise in the Neville *et al.* study, in our view, is the similarity between the regions activated within the left hemisphere by sign language in deaf individuals compared with those activated by spoken language (written or auditory) in hearing individuals. Despite its visuospatial 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 cortices involved in processing ASL? Why not visual-related cortices? Why is Broca's area, which is conveniently situated just anterior to that portion of the motor cortex controlling speech-related musculature, activated in sign language processing? Why isn't the functional equivalent of Broca's area shifted more superiorly 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 parietal lobe's spatial and visuo-motor functions³, yet it showed no significant activations. Apparently traditional left perisylvian language areas are involved in processing not just speech, but language, defined more abstractly. Lesion data concerning the left hemisphere organization of ASL support this view^{1,23}.

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, the dorsal aspect of the temporal lobe, which includes the transverse temporal (or Heschl's) gyrus and the planum temporale. This region is uniformly activated in hearing subjects listening to spoken language^{17,18,24} 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 signer²⁵.

One potential explanation for this is that supratemporal plane structures are involved in processing non-linguistic auditory information²⁶: 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 yet know for sure. 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. Save 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 biases (or both) remains to be seen. Provocative issues indeed.

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Response from Corina, Neville and Bavelier

The commentary by Hickok, Bellugi and Klima¹ raises several issues regarding our recently published functional neuroimaging study of native deaf and hearing signers processing American Sign Language (ASL) and English². 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 native signers, they also reveal considerable 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 processing³. We maintain that this RH activity reflects language processing requirements of a signed language which are not observed in the processing 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.

Examining the patterns of activations observed for written English and for ASL processing, we have argued that the early acquisition of a natural language is important in the expression of the strong bias for left-hemi-

sphere areas to mediate language, independent of the form of the language. In addition, the extensive activation of the right hemisphere reflects that the specific processing requirements 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 left-hemisphere structures in the mediation of signed languages. We differ, however, with respect to the relative importance of the extensive RH activation observed in the fMRI study of ASL processing. It is important to note that several groups using PET and fMRI techniques have reported RH activation of temporal and frontal areas in response to spoken language processing 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 language experiments the RH activity is never as statistically robust as the left-hemisphere activity. In our study, the RH activation of native signers in the ASL condition was as robust as that observed 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

right-hemisphere Broca's area homologue and dorsolateral prefrontal cortex. This suggests that specialization of these frontal areas for language processing may be dependent upon difference in sensory input at formative points in development. Taken together, the differences in degree and extent of activation observed in the ASL studies and the within group differences reported (hearing native signers versus deaf native signers) leads us to believe that no single factor will sufficiently account for the RH activity observed when native signers process ASL.

In their discussion of this work, Hickok et al. suggest that the robust RH activation observed in the ASL study is an artifact of the comparisons of these data with a condition of written English processing. It should be made clear that the written English task was never intended to serve as a control condition for the ASL condition. One goal of this initial study was to provide at least a within-modality (i.e. visual) comparison of language processing across these separate studies and groups of subjects. In our studies, the processing of written English is contrasted with the processing of meaningless consonant strings. In the ASL condition, ASL signing is contrasted with the processing of fluent non-sign 'gibberish', produced by the same signing model. Hickok et al. note that the presence of information such as facial expression, and non-linguistic gesture in the signing conditions may account for the observed differences in RH activation. As noted, in our experiment, facial information and non-linguistic gesture are common in both the ASL and sign-gibberish stimuli and thus cannot be responsible for the RH activity observed. This point is made clear in the comparison of the hearing non-signers who showed no consistent activation when viewing the alternation between ASL and non-sign gibberish. This finding provides

D.P. Corina is at the
Department of
Psychology,
University of
Washington, Seattle,
WA 98195, USA.

tel: +1 206 543 4588
fax: +1 206 685 3157
e-mail: corina@u.
washington.edu

H.J. Neville is at the
Department of
Psychology,
University of
Oregon, Eugene,
OR, USA.

D. Bavelier is at
Georgetown Institute
for Cognitive and
Computational
Sciences, Washington,
D.C., USA.