The neural organization of language: evidence from sign language aphasia

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To what extent is the neural organization of language dependent on factors specific to the modalities in which language is perceived and through which it is produced? That is, is the left-hemisphere dominance for language a function of a linguistic specialization or a function of some domain-general specialization(s), such as temporal processing or motor planning? Investigations of the neurobiology of signed language can help answer these questions. As with spoken languages, signed languages of the deaf display complex grammatical structure but are perceived and produced via radically different modalities. Thus, by mapping out the neurological similarities and differences between signed and spoken language, it is possible to identify modality-specific contributions to brain organization for language. Research to date has shown a significant degree of similarity in the neurobiology of signed and spoken languages, suggesting that the neural organization of language is largely modality-independent.

While the left cerebral hemisphere’s dominance for language is well-established, the basis of this asymmetry is still a matter of debate. Some have argued that the left hemisphere contains neural systems specialized for processing linguistic information, while others have claimed that the left hemisphere systems are not specialized for language processing per se, but rather for a more domain-general process, or set of processes. On the latter view there is no direct neurobiological association between language itself and the left hemisphere except insofar as language processes involve these more basic, domain-general operations. There have been two principle candidates proposed for a domain-general basis for language asymmetry: (1) processing of rapidly changing temporal information, and (2) controlling the articulation of complex motor sequences. To be sure, processing language involves neural mechanisms such as these to some extent, and there is evidence to suggest that an impairment in fast temporal processing or articulation of motor commands can affect aspects of language performance, at least under some conditions. However, in this paper, we review data that call into question the hypothesis that left hemisphere dominance for language can be reduced fully to domain-general processes.

The data come from studies of deaf individuals who have unilateral brain lesions and whose primary means of communication is American Sign Language (ASL). This population provides a means to examine the neurobiology of a natural, highly structured human language (see Box 1) with modality dependent effects (such as a heavy reliance on processing fast temporal information) factored out, and thus is well-suited to addressing questions concerning the basis of brain organization for language generally.

In discussing the neural organization of language, it is worthwhile clarifying at the outset exactly which aspects of language we are talking about. Language is a complex, multi-level system. One can talk about phonological, morphological and syntactic processes, as well as lexical, semantic, discourse and pragmatic-level processes, among others. When it is claimed that ‘language’ is predominantly processed by the left hemisphere, this usually refers to phonological, morphological and syntactic levels (what can be called grammatical structure) as well as aspects of lexical-semantic processing. Unless otherwise indicated, we will follow this convention when we refer to ‘sign language’.

The signs of aphasia

A number of case studies have suggested that in deaf life-long signers the left hemisphere is dominant for comprehension and production of signed language (5, 6). (See also previous case study reviews (7, 8).) In these studies, left-hemisphere damaged (LHD) signers presented with disruptions in various aspects of their signing ability (aphasia) whereas right-hemisphere damaged (RHD) signers were non-aphasic. Here, we provide some examples of the types of sign language deficits found in individual cases which make the point that the kinds of deficits observed in deaf signers are quite similar to those found in hearing aphasia. We will then turn to...
group-level studies comparing the effects of left versus right-hemisphere damage on sign language ability.

Case studies
(1) Paraphasic errors: a hallmark of aphasia is the presence of paraphasic errors in language production. Several types of paraphasic errors occur to varying degrees in different types of aphasia. These include ‘ literal’ or ‘ phonemic’ paraphasias in which errors are made in the sound pattern of words (e.g. ‘ tag ’ for ‘ table ’), ‘ verbal’ or ‘semantic’ paraphasias in which a semantically related word is substituted for the target (e.g. ‘ uncle’ for ‘ brother ’), and ‘ paragrammatic’ paraphasias in which inappropriate or neologistic words or morphemes are selected during running speech. A similar range of paraphasic errors have been documented in many of the LHD signs that have been studied. Some examples of phonemic

Box 1. Sign language as a natural human language

**A. Spatial contrasts at the lexical level**

- Summer
- Ugly
- Dry

**B. Spatially nested morphology**

- GIVE (uninflected)
- GIVE [durational] (give continuously)
- GIVE [exhaustive] (give to each)

- GIVE [exhaustive] [durational] (give continuously to each in turn, that action recurring over time)
- GIVE [[durational] [exhaustive]] [durational] (give continuously to each in turn, that action recurring over time)

**Fig. A,B Spatial contrasts at the lexical and morphological levels in ASL.** (A) The same sign at different spatial locations has three different meanings. (B) Different inflections of the word ‘give’, shown by increasing sign complexity. (Reproduced, with permission, from Ref. 15.)
and paragrammatic paraphasias produced by LHD signers are shown in Fig. 1. Note that the phonemic errors (Fig. 1A) represent a substitution of one ASL phoneme for another, whereas the paragrammatic error (Fig. 1B) represents an illegal combination of ASL morphemes, the root sign ‘brilliant’ combined with the grammatical inflection that conveys a meaning similar to ‘characteristically.’ Errors like these are fairly common in LHD signers, but not in RHD signers.

(2) Fluent and non-fluent aphasias: the distinction between fluent and non-fluent aphasias (defined in terms of the number of words uttered in an uninterrupted string) is prominent in aphasia research and appears to be a fairly robust dichotomy. This distinction has also been observed in sign language aphasia. One subject presented with a Broca’s-aphasia-like syndrome in which her sign output was extremely effortless, dysarthric, and restricted to one or two
signs at a time (mostly nouns); comprehension was relatively spared. Consistent with data from hearing aphasics, her lesion involved most of the left lateral frontal lobe. A contrasting case sustained a mostly posterior lesion. He was able to string together sequences of several signs effortlessly, but he produced frequent paraphasic errors including several paragrammatical errors. 

(3) Naming: a virtually universal symptom of aphasia is a difficulty in retrieving words; a deficit that is often revealed when subjects are asked to provide the name for pictured objects or actions7. This appears to be true also for sign language aphasia: on a 52-item naming test RHD subjects correctly named an average of 31.1 items (range 30–32). LHD subjects correctly named an average of 25.2 items (range 12–32), with 61% scoring below the RHD range. Excluding LHD subjects with non-perisylvian or subcortical lesions the percentage of subjects scoring below the RHD range increased to 80% (8/10), and one of the two subjects who performed well on the naming task had marked ‘sign finding’ problems during conversational production. Difficulty in naming, then, appears to be a pervasive symptom of sign language aphasia, just as it is in spoken language aphasia. 

(4) Grammaticism: a common feature of aphasia produced by anterior left perisylvian lesions is grammaticism, a tendency to omit grammatical function morphemes in speech7. A similar deficit has been observed in a Broca’s aphasia-like subject6. Her production, in addition to being severely non-fluent, lacked all of the syntactic and morphological markings required in ASL. 

(5) A case of ‘sign blindness’: ‘pure word blindness’ or ‘alexia without aphagria’ has been well-documented in the literature9. Patients with this disorder have normal spoken and heard language capacity; are able to write, but cannot read even their own writing. The lesion typically involves the left primary visual cortex and splenium of the corpus callosum. Language areas are preserved, allowing normal production, comprehension and writing, but these areas are isolated from visual input. A recently reported deaf signer had such a lesion and was alexic as expected9. Would her signing be similarly affected? The answer was indeed yes. Her signing was fluent and grammatical, yet her comprehension was profoundly impaired; she could not follow even simple one-step ASL commands: Visual object recognition, however, was unimpaired. It would appear that this patient was essentially blind for sign language as a result of her left medial occipito-temporal lesion that isolated the left hemispheric language systems from visual information. This case provides strong evidence favoring the view that the left hemisphere is dominant for ASL in deaf individuals because it demonstrates that the right hemisphere by itself has little capacity to process signed language beyond rudimentary single-sign comprehension. 

(6) Double dissociation: a recent group study comparing 13 LHD and 10 RHD signers on a range of standard language tests has confirmed the hypotheses suggested by case studies that the left hemisphere is dominant for sign language10. Using an ASL-adapted version of the Boston Diagnostic Aphasia Examination11, this study assessed each subject’s competence in several basic aspects of language use: production, comprehension, naming and repetition. 

The LHD signers performed significantly worse than the RHD signers on all measures. The differences held even in the subset of subjects who were both deaf from birth and were exposed to ASL prelingually (3 RHD, 5 LHD).
Crucially, this subset of cases includes contrasting LHD and RHD subjects with large perisylvian lesions.

(2) Non-linguistic spatial cognitive assessment: it was noted above that a double-dissociation has been documented between sign language deficits and deficits in non-linguistic visuospatial abilities. The visuospatial abilities that were assessed in that work involved relatively gross, global disruptions (see Fig. 2) of the type that are typically associated with right-hemisphere damage. While these data make the point that there is a fair degree of separability between language and gross visuospatial function, they do not address the question of whether more subtle visuospatial deficits -- of the type commonly associated with left-hemisphere damage in the hearing/speaking population -- might underlie sign language deficits. A recent experiment addressed this issue.

A group of left- or right-lesioned deaf signers were asked to reproduce drawings that contained hierarchically organized structure. Consistent with data from hearing subjects, LHD deaf subjects were significantly better at reproducing global-level features (global configuration) whereas RHD deaf subjects were significantly better at reproducing local-level features (internal details). However, local-level visuospatial deficits in LHD signers did not correlate with expressive or receptive sign language measures. These findings suggest that language deficits in LHD deaf signers cannot be attributed to domain-general visuospatial deficits.

Within hemisphere organization of signed language

Given that the sensory/motor and input/output systems are radically different in signed versus spoken language, one might expect significant reorganization of within-hemisphere areas involved in signed language processing. For example, it seems reasonable to suppose that regions involved in sign language perception would be located in visual association cortex rather than in auditory association cortex as is the case for spoken language. Likewise, one might hypothesize that signed language production would involve pre-motor regions anterior to the part of motor cortex representing hand and arm, rather than anterior to motor cortex for the oral articulators, where Broca’s area is. Given the sparseness of the clinical population, this is a difficult issue to address using the lesion approach but some preliminary data on the issue have emerged.

To the extent that the types and patterns of deficits found in aphasia for sign language are similar to those found in aphasia for spoken language, a common functional organization is suggested between the two forms of language within the left hemisphere. There do seem to be a number of commonalities in the language deficits found in signed and spoken language: Thus, many of the aphasic symptom clusters that have been observed in deaf signers fall into classical clinical categories defined on the basis of hearing aphasics, and the lesions producing these patterns of deficits in LHD signers are consistent with clinical-anatomic correlations in the hearing population. Examples of this include the following observations: there has not been a case in which a lesion outside the perisylvian language zone has led to a primary aphasia (although admittedly there have not been many subjects with extra-perisylvian lesions); non-fluent aphasic signers have lesions involving anterior language regions, and fluent aphasic signers have lesions involving posterior language regions; and Broca’s area appears to play a role in ASL production (see Box 2). In addition, the range of common deficit types that have been reported in hearing aphasics have been observed regularly in sign language aphasia (see above). Thus, based

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**Fig. 2** Performance on spatial cognitive tasks by four aphasic LHD signers (top) and four non-aphasic RHD signers (bottom). The task in each case was to copy the model drawing in the centre panel. RHD signers show a greater impairment than LHD signers, indicating a dissociation between language and non-linguistic visuospatial functions. (Reproduced, with permission, from Ref. 15.)
Box 2. The role of Broca's area in sign language production

Broca's area has figured prominently in hypotheses concerning the anatomy of speech production. While recent studies have shown convincingly that lesions contralateral to Broca's area do not lead to a lasting, severe speech production deficit, evidence from the acute poststroke syndrome, from cortical stimulation, and from functional neuroimaging suggests at least some role for Broca's area in speech production. The idea that Broca's area is involved in speech production holds considerable intuitive appeal—it makes sense that an area involved in 'programming' speech should be topographically situated near motor cortex controlling speech-related musculature. In fact, it is tempting to hypothesize that the location of motor cortex for the speech articulators is what drives the topographic organization of Broca's area (functionally speaking) in development. Determining whether Broca's area (anatomically speaking) plays a role in the production of sign language (which uses articulators that are controlled by superior-lateral motor cortex) will contribute to answering the question: To what extent is the central organization of language areas driven by the control topography of the sensory–motor systems?

Relevant to this question is a recent case study of a congenitally deaf, native user of ASL, who suffered an ischemic infarct involving Broca's area and the inferior portion of the primary motor cortex (see Fig.). This study revealed both similarities and differences in the aphasia syndrome compared with that found in hearing/speaking subjects following such a lesion. In short, the set of symptoms observed in the case of sign language aphasia was a superset of that noted in spoken language: consistent with the effects of similar lesions in hearing subjects, the deaf subject presented with an acute mutism that quickly resolved. But whereas hearing subjects are typically left with only a mild aphasia, or no aphasia at all, the deaf subject was left with a chronic fluent aphasia characterized by frequent phonemic paraphasias. These findings suggest that Broca's area does indeed play a role in sign language production, which in turn suggests that at least some aspects of the within-hemisphere organization of language must be modality independent.

Functional dissociations

Here we describe a number of functional dissociations that shed light on the relation between language and other cognitive domains. The first two concern the separability of sign language deficits from non-linguistic processes that involve the manual modality—namely, manual praxis and general ability—and the third examines the use of space to represent linguistic information in ASL (as in identifying the subject and object of a sentence) compared with the use of space to represent spatial information itself.

On the relation between apraxia and aphasia

Dissociations between motor control in the service of sign language versus the service of non-linguistic behaviors have been reported by several authors. Some of these data come from fine-grained analyses of the effects of Parkinson's disease (PD) on deaf signers. Potter and colleagues report that while signers with PD exhibit disruptions in temporal organization and coordination during sign production, linguistic distinctions are preserved in contrast to aphasic signers. Other workers, however, have reported an association between sign language disruptions and disruptions of domain-general motor control which has led to the claim that sign aphasia is merely a reflection of apraxia. To address this claim a group of LHD signers were asked to copy non-representational manual movements using the arm ipsilateral to the lesion. Varying degrees of disruption in the ability to perform this task were noted, but apraxia scores did not correlate significantly with measures of sign production during connected signing. 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 motor control.
Dissociation of gesture and sign language
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. Following an ischemic infarct involving both anterior and posterior perisylvian regions, the subject became aphasic for sign language. His comprehension was poor and his sign production was characterized by frequent paraphasias and a tendency to substitute pantomimes 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 the sign language deficit. A similar dissociation was noted in his comprehension of signs versus pantomime. 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.

Use of space in communicative grammatical information versus spatial information directly
In addition to using space to encode grammatical information, ASL uses space to represent spatial information directly, as for example, in describing the layout of objects in a room. It is worth making the distinction clear between the grammatical use of space in ASL, as in the encoding of phonological, morphological, and syntactic information described previously, and the use of space to encode spatial information directly in ASL discourse. The latter refers to the ability to use language to communicate spatial information, and it takes place in signed and spoken language. Spoken language communicates spatial information through the use of prepositions and spatial description words as in, 'The cup is on the left, front corner of the table.' Note that the grammatical structure of such a sentence is independent of how accurate the spatial information is. In ASL, instead of using lexical means to communicate spatial information, in many cases the notation of objects relative to one another is literally mapped out in (signing) space. Again, the grammatical structure of a signed sentence is independent of the truth value of the content.

Can the grammatical use of space (i.e. language) be dissociated from the use of space to communicate spatial information (i.e. spatial cognition) even when these types of information are expressed in the same channel? Two deaf, native signers—one LHD and one RHD—participated in a comprehension task involving these two uses of space within ASL. The grammatical task involved signed sentences similar to, 'the cat chased the dog' in which the grammatical subject and object of the verb were indicated spatially. The spatial task involved a signed description of the layout of furniture in a room. In both tasks, subjects were asked to match the signed stimulus to a picture. The LHD signer was impaired on the grammatical task, but performed well on the 'spatial' task. The RHD signer showed the reverse pattern. These data suggest that the neural organization of language and spatial cognition are driven by the type of representation that is ultimately constructed from the signal (grammatical versus spatial), rather than by the physical properties of the signal itself.

Neuropsychology of sign language as revealed by functional neuroimaging
Recent studies have begun looking at the neural organization of sign language using various functional imaging techniques. One such study addressed the question, 'Does Broca’s area play a role in sign language production?' Native deaf signers participated in a functional magnetic resonance imaging (fMRI) experiment in which they covertly produced ASL signs. Similar tasks (including covert production) have produced fMRI activations in Broca’s and Wernicke’s areas in hearing subjects producing spoken words. In preliminary analyses it was found that deaf subjects did indeed show activation in Broca’s area (G. Hickok et al. reported at Society for Neuroscience, 1995), corroborating earlier lesion work.

Another recent fMRI study carried out by Neville and colleagues has provided further evidence that classic left-hemisphere language regions are activated during the perception of ASL sentences by deaf native signers. And event-related potential (ERP) work has also suggested that the within-hemisphere organization of neural systems mediating grammatical and lexical aspects of signed and spoken language are quite similar. Taken together, these recent neuroimaging studies corroborate the lesion data and suggest that at least some major components of the neural organization for language processing are modality independent.

There has been the additional suggestion, based primarily on some of the above mentioned neuroimaging work, that while classic left-hemisphere language areas are involved in sign language production and comprehension, there may be more extensive involvement of right-hemisphere systems in processing signed compared to spoken language, a claim that appears contradictory to what has been concluded based on lesion work. There are several possible explanations for this discrepancy. The first is that the functional imaging studies contrasted deaf subjects perceiving sign language sentences, with hearing subjects reading printed English sentences. Thus, the conditions differ in (1) their prosodic content, a right-hemisphere language function; and (2) the visual presence of a human source for the linguistic signal which may have included non-linguistic communicative signals as well. Secondly, the sign stimuli used in these studies may have incorporated some of the spatial description mechanisms described above, which could have driven right-hemisphere systems. A final, more general point is that lesion studies often target specific behaviors (e.g. naming ability, phonological processing, etc.) and ignore others (e.g. discourse, prosodic abilities), whereas an imaging study may reflect processes across a wider range of linguistic and non-linguistic domains simultaneously. It is therefore difficult to know which aspect(s) of the stimulus, or higher-level cognitive operation on the stimulus, is driving the additional activations (e.g. deaf people might use visual imagery to a greater extent during language processing). Therefore, much work remains to be done before strong conclusions can be drawn from these neuroimaging studies regarding possible differences in the hemispheric organization of signed and spoken language, but the general claim regarding the involvement of classic left-hemisphere systems in deaf signers has been confirmed by these results.
Outstanding questions

• Language processes appear to be separable from domain-general processes in the adult. Might these domain-general processes contribute to language organization in development or perhaps in evolution?
• How do lower-level visual perception systems, such as those involved in processing motion and shape, interact with the perception of movement and hand-shape components of signed utterances?
• What neural pathways are involved in the transmission of information from the visual system to temporal lobe language systems in sign language perception? Might these pathways overlap with those involved in the perception of the printed form of spoken language by hearing-speaking individuals?
• Will it be possible to ‘treat’ a patient with ‘sign blindness’ by training them to perceive sign language in the tactile modality, as is done with deaf-blind individuals? The analysis of ‘sign blindness’ presented above predicts that this should be possible.

Conclusion
Research investigating the neural organization of signed language and spatial cognition in deaf individuals has demonstrated the same hemispheric asymmetries found in hearing, speaking individuals. This suggests that the hemispheric organization of grammatical aspects of language is independent of modality and, more specifically, unaffected by the fact that signed language involves a significant degree of visuospatial processing. Recent investigations of the within-hemisphere organization of sign language have hinted that there is also a similar degree of similarity in the neural organization of signed and spoken language even within the left hemisphere, although much work remains.

Since the time-course of sign language articulation is significantly slower than for spoken language, the existence of sign language deficits following left-hemisphere damage argues against the view that the lateralization of language is simply a function of a more general left-hemisphere bias for rapid temporal processing. Further, a series of functional dissociations has shown that deficits in processing sign language cannot be explained in terms of other domain-general deficits such as manual praxis and symbolic communication (pantomime). Finally, dissociations within aspects of sign language and between sign language and non-linguistic spatial abilities (all of which might fall under the general rubric of ‘visuospatial processing’) suggest that the functional organization of cognitive systems is in some extent modular, with the ‘modules’ being organized with respect to representational properties of the systems (e.g. grammatical representations versus purely spatial representations), rather than in terms of the physical characteristics of the stimulus (e.g. visuospatial versus temporal).

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