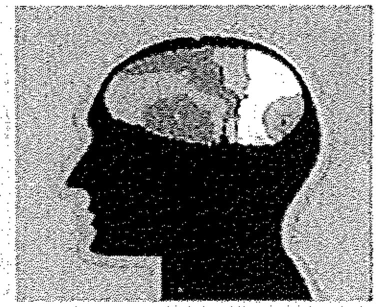
NEUROSCIENCE,
MEMORY, AND LANGUAGE



DECADE OF THE BRAIN

Clues to the Neurobiology of Language

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CLUES TO THE NEUROBIOLOGY OF LANGUAGE

Ursula Bellugi and Gregory Hickok

In the Decade of the Brain, we stand at a new frontier in our ability to understand the biological foundations for language and other higher cognitive functions. The techniques currently available are powerful and exciting, as well as rapidly expanding. A number of techniques that were simply not available a decade ago permit us to gain precise information on the neural systems that subserve cortical functions by eavesdropping on brain structure and brain function. New studies using functional imaging (positron emission tomography, or PET among others) are telling us where in the brain linguistic and cognitive processing takes place on-line; new techniques using three-dimensional reconstruction of magnetic resonance images (MRI) now allow us to visualize directly the living brain as if we were holding it in our hands.

This three-dimensional computer reconstruction can be sliced and resliced along any dimension an infinite number of times, permitting quantitative morphological analysis in the normal brain and precise localization of nonfunctional regions in the damaged brain. Just recently, functional imaging and MRI-derived three-dimensional reconstructions have been integrated to give us three-dimensional reconstructions of the living active brain while it is engaged in cognitive activities. In the context of these and other technological advances in the Decade of the Brain, we describe a program of studies, illuminated by new techniques in brain imaging, leading toward a deeper understanding of the neural systems that subserve language and other higher cognitive functions.

Using a multidisciplinary approach we seek to gain insight into the often inaccessible workings of the brain, studying unusual languages and populations with differing cognitive and language abilities. Most of what is known about language comes from the study of spoken languages. In contrast, we have addressed dramatically different languages: the visual forms of communication that have arisen outside of the mainstream of spoken languages. In these studies, we investigate language, its formal architecture, and its representation in the brain by studying the visual gestural systems developed among generations of deaf people. American Sign Language (ASL) displays complex linguistic structure, but, unlike spoken languages, ASL conveys much of its structure by manipulating spatial relations, thus presenting a new perspective on the determinants of language organization. This research program involves functional and structural brain imaging and the application of new experimental paradigms to determine how language is acquired, processed, and represented within the brain.

Perspectives from Language in a Different Modality

The central issues we address, namely brain organization for language and other higher cortical functions, have been illuminated by some new discoveries about the nature of language itself. Because, until recently, most of the scientific understanding of language has come from the study of spoken languages, experimental findings concerning the neural instantiation of language necessarily pertained to neurolinguistic systems only as they relate to auditory and phonetic processing. In fact, the organizational properties of language have been assumed to be connected inseparably with the sounds of speech. It has been assumed that the fact that language is normally spoken and heard determines the basic principles of grammar as well as the organization of the brain for language. Studies of brain organization indicate that the left cerebral hemisphere is specialized for processing linguistic information in the auditory-vocal mode; thus, the link between biology and behavior has been identified with the particular sensory modality in which language has developed.

Although evolution in humans has been for spoken language (there is no group of hearing people that has a sign language as its primary linguistic system), recent research into sign languages has revealed the existence of primary linguistic systems that have developed naturally in visual/manual modalities. These signed languages have all of the complexity of spoken languages and are passed down from one generation of deaf people to the next. Importantly, these sign languages are not derived from the spoken language of the surrounding community; rather, they are autonomous languages with their own grammatical form. Indeed, the sign language developed by deaf people in Great Britain is

mutually incomprehensible with the sign language developed among deaf people in the United States. The existence of these visual/manual primary linguistic systems can provide a new perspective on the determinants of brain organization for language. How is language organized when it is based instead on moving the hands in space and on visual processing? We can now investigate how the brain is organized for language when language itself is instantiated in space.

American Sign Language (ASL) exhibits formal structuring at the same levels as spoken languages and the same kinds of organizational principles as spoken languages. At the core, spoken and signed languages are essentially identical in terms of rule systems. Nevertheless, on the surface, signed and spoken languages differ markedly. The formal grammatical structuring assumed in a visual/manual language is influenced deeply at all structural levels by the modality in which the language is cast. ASL displays a complex linguistic structure, but unlike spoken languages, it conveys much of its structure by manipulating spatial relations, making use of spatial contrasts at all linguistic levels.

In our research, we have been specifying the ways in which the formal properties of language are shaped by their modalities of expression, sifting properties peculiar to a particular language mode from more general properties common to all languages. As noted, the most striking surface difference between signed and spoken languages is the reliance on spatial contrasts, most evident in the grammar of the language. Figure 1 shows some aspects of grammatical structure in ASL and its reliance on spatial contrasts. Instead of relying on linear order for inflectional marking, as in English (*act, acting, acted, acts*), ASL grammatical processes nest sign stems in spatial patterns of considerable complexity, thereby marking grammatical functions such as number, aspect, and person. Grammatically complex forms can be spatially nested, one inside the other, with different orderings producing different meanings (figure 1A). Similarly, the syntactic structure specifying relations of signs to one another in sentences in ASL is also essentially spatially organized. Nominal signs may be associated with abstract positions in a plane of signing space, and the direction of movement of the verb signs between such endpoints marks grammatical relations. Pronominal signs directed toward these previously established loci clearly function to refer back to nominals, even with many signs intervening (figure 1B). This spatial organization underlying syntax is a unique property of visual-gestural systems.

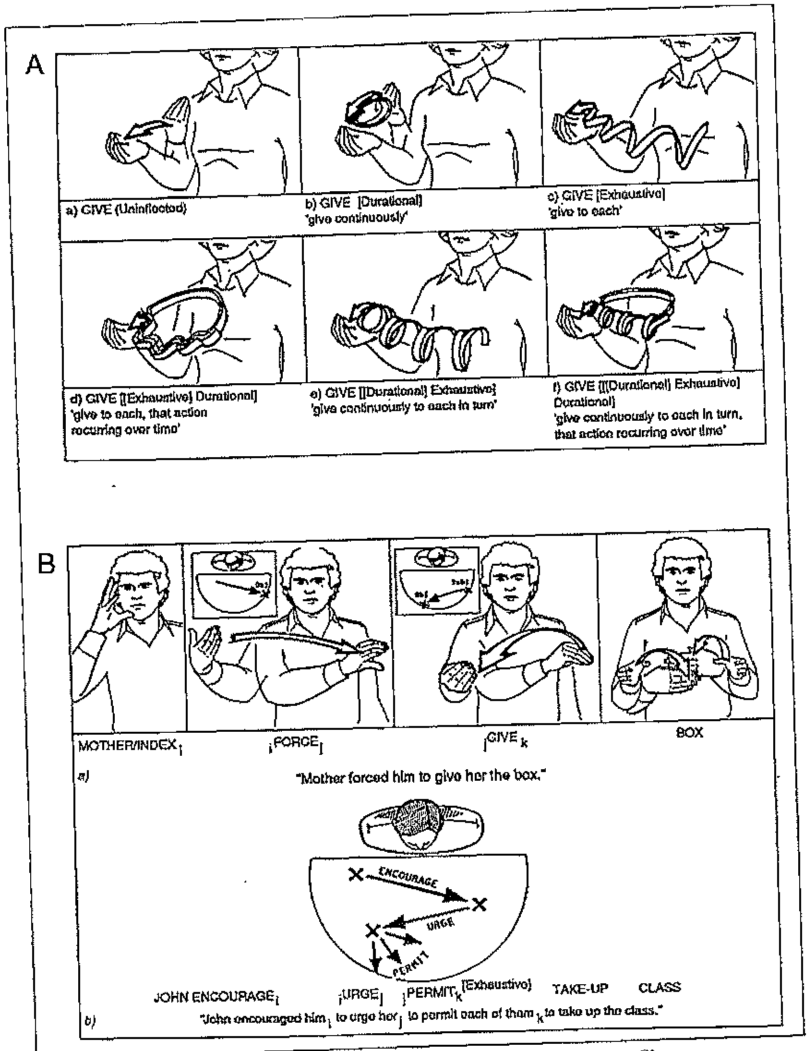


Figure 1. Spatially organized morphology and syntax in American Sign Language. (TINS)

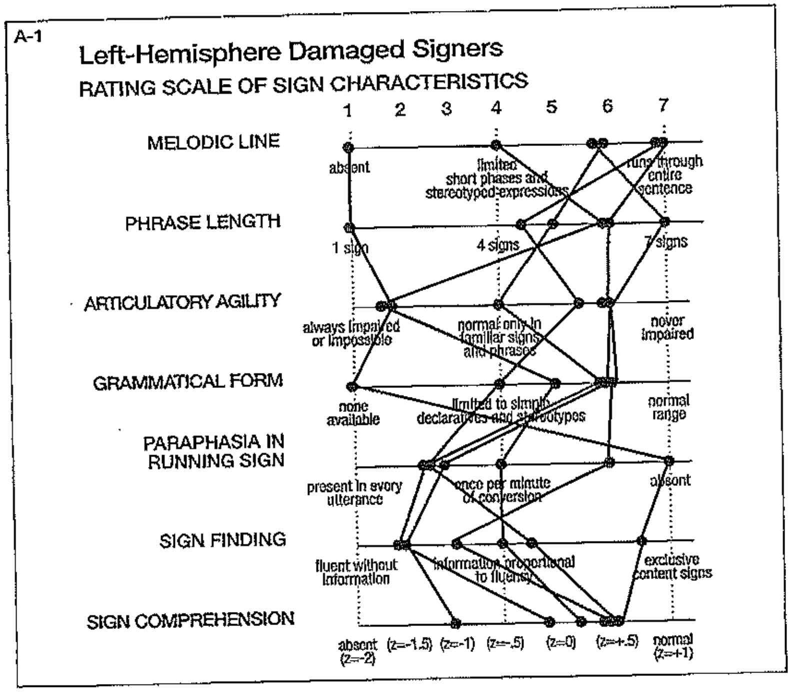
Neural Systems Subserving a Visuospatial Language

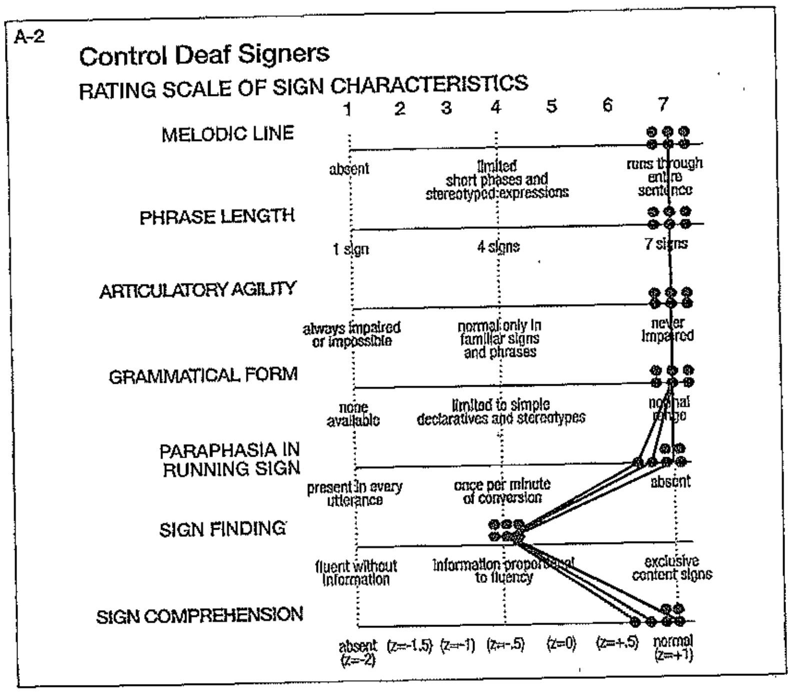
Not only is sign language independent from spoken language, it is transmitted in a different modality and encodes linguistic structure in essentially spatial distinctions rather than temporal distinctions. These differences between signed and spoken languages provide an especially powerful tool for understanding the neural systems subserving language. Consider the following: In hearing/speaking individuals, language processing is mediated by the left cerebral hemisphere, whereas visuospatial processing is mediated by the right cerebral hemisphere. But what about a language that is communicated using spatial contrasts rather than temporal contrasts?

On the one hand, the fact that sign language has the same kind of complex linguistic structure as spoken languages and the same expressivity might lead one to expect left hemisphere mediation. On the other hand, the spatial medium so central to the linguistic structure of sign language clearly suggests right hemisphere mediation. The answer to the question raised is dependent on the answer to another deeper question concerning the *basis* of the left hemisphere specialization for language. Specifically, is the left hemisphere specialized for language processing per se (i.e., is there a brain basis for language as an independent entity)? Or is the left hemisphere's dominance generalized to processing any type of information presented in terms of temporal contrasts?

If the left hemisphere is indeed specialized for processing language itself, sign language processing should be mediated by the left hemisphere just as spoken language is. If, however, the left hemisphere is specialized for processing fast temporal contrasts in general, we would expect sign language processing to be mediated by the right hemisphere. The study of sign languages in deaf signers permits us to pit the nature of the signal (auditory/temporal vs. visual/spatial) against the type of information (linguistic vs. nonlinguistic) encoded in that signal as a means of examining the neurobiological basis of language.

We address these questions through a large program of studies of deaf signers with focal lesions to the left or the right cerebral hemisphere. We investigate several major areas, each focusing on a special property of the visual-gestural modality as it bears on the investigation of brain organization for language. We have now studied intensively more than twenty deaf signers with left or right hemisphere focal lesions; all are highly skilled ASL signers, and all have used sign as a primary form of communication throughout their lives. Our subjects are examined with an extensive battery of experimental probes, including formal testing of ASL at all structural levels; spatial cognitive probes sensitive to right hemisphere damage in hearing people; and new methods of brain imaging. This large pool of well-studied and thoroughly characterized subjects allows a new perspective on the determinants of brain organization for language.





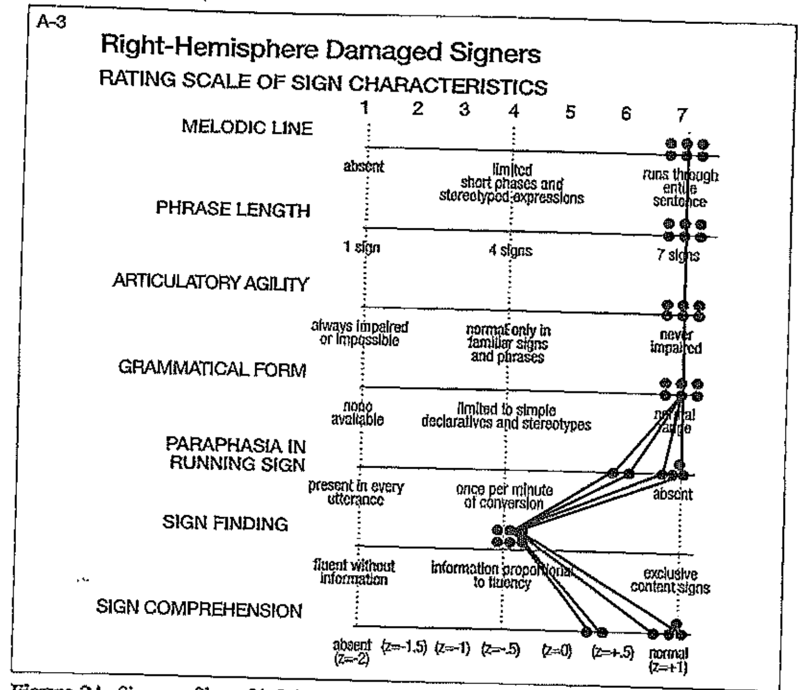


Figure 2A. Sign profiles of left-lesioned signers (A-1), right-lesioned signers (A-3), and the control group (A-2).

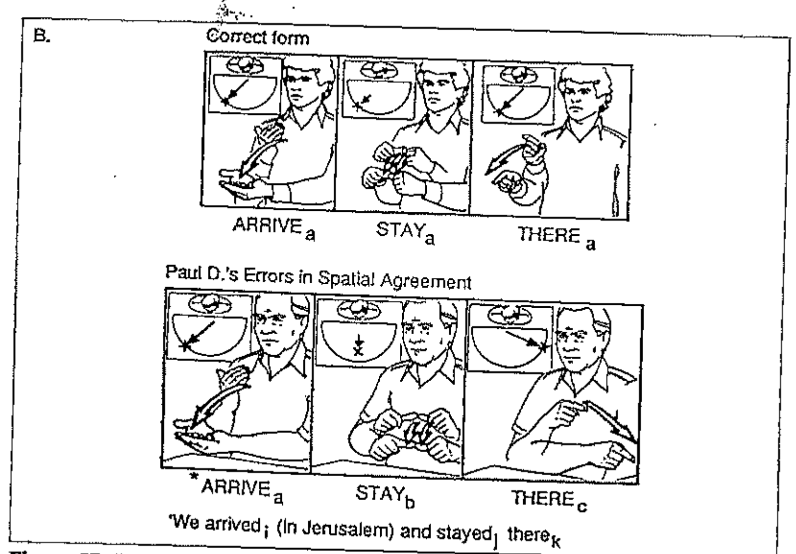


Figure 2B. Impairment in spatially organized syntax in left-lesioned signers.

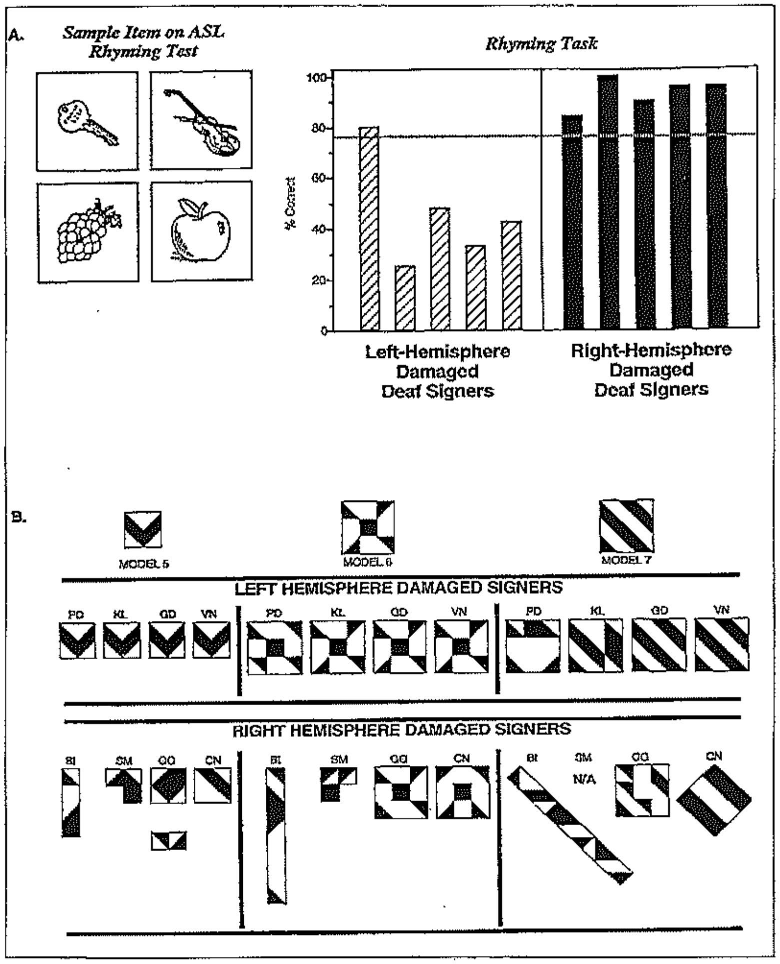


Figure 3. The contrast between language and nonlanguage spatial processing in left- and right-lesioned signers. (A) Phonological processing is impaired in LHD but not RHD. (B) Block design is impaired in RHD but not LHD.

Left-Hemisphere Lesions and Sign Language Grammar

Our first major finding is that only deaf signers with damage to the left hemisphere show sign language aphasias. Marked impairment in sign language after left-hemisphere lesions was found in the majority of the left-hemisphere damaged (LHD) signers but not in any of the right-hemisphere damaged (RHD) signers, whose language profiles were much like matched controls. Figure 2A pre-

sents a comparison of LHD, RHD, and normal control profiles of sign characteristics from our Sign Diagnostic Aphasia Examination—a measure of sign aphasia. The RHD signers showed no impairment in any aspect of ASL grammar; their signing was rich, complex, and without deficit, even in the spatial organization underlying sentences of ASL. By contrast, signers with LHD showed markedly contrasting profiles: one was agrammatic after her stroke, another made frequent paraphasias at the sign internal level, and a third showed grammatical paraphasias, particularly in morphology. A fourth deaf signer showed deficits in the capacity to perform the spatially encoded grammatical operations which link signs in sentences, a remarkable failure in the spatially organized syntax of the language (figure 2B). In contrast, none of the RHD signers showed any within-sentence deficits; they were completely unimpaired in sign sentences and not one showed any hint of aphasia for sign language (in contrast, however, to their marked nonlanguage spatial deficits, described below).

Moreover, we find dramatic differences in performance between left- and right-hemisphere damaged signers on formal experimental probes of sign competence. For example, we developed a test of the equivalent of rhyming in ASL, a probe of phonological processing. Two signs "rhyme" if they are similar in all but one phonological parametric value such as handshape, location, or movement. To tap this aspect of phonological processing, subjects are presented with an array of pictured objects and asked to pick out the two objects with signs that rhyme (figure 3A). Left-hemisphere damaged signers are significantly impaired relative to RHD signers and controls on this test, another sign of the marked difference in effects of right and left hemisphere lesions on signing. On other tests of ASL processing at different structural levels, we found similar distinctions between left- and right-lesioned signers, with the right-lesioned signers much like the controls, but the signers with left-hemisphere lesions significantly impaired.

Right-Hemisphere Lesions and Spatial Processing

These results from language testing contrast sharply with results on tests of nonlanguage spatial cognition. The RHD signers are significantly more impaired on a wide range of spatial cognitive tasks than LHD signers, who show little impairment. Drawings of many of the RHD signers (but not those with LHD) show severe spatial distortions, neglect of the left side of space, and lack of perspective. Figure 3B presents samples of RHD versus LHD signers' performance on a

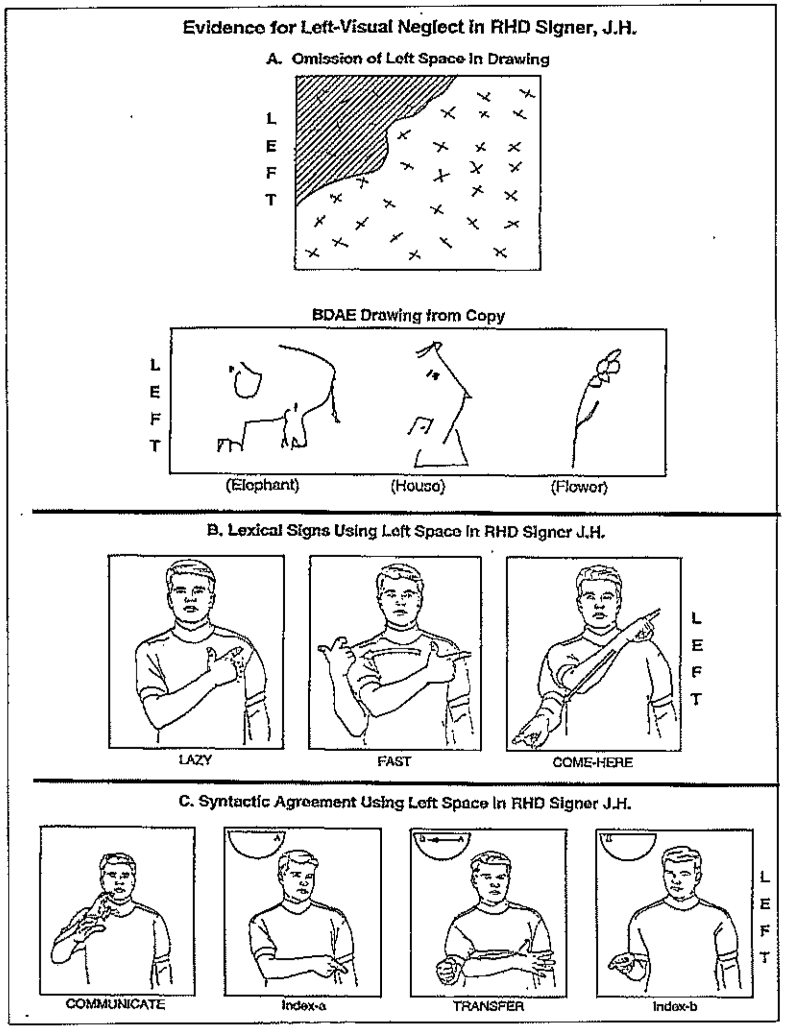


Figure 4. Neglect for spatial cognition but not sign language in a right-lesioned signer.

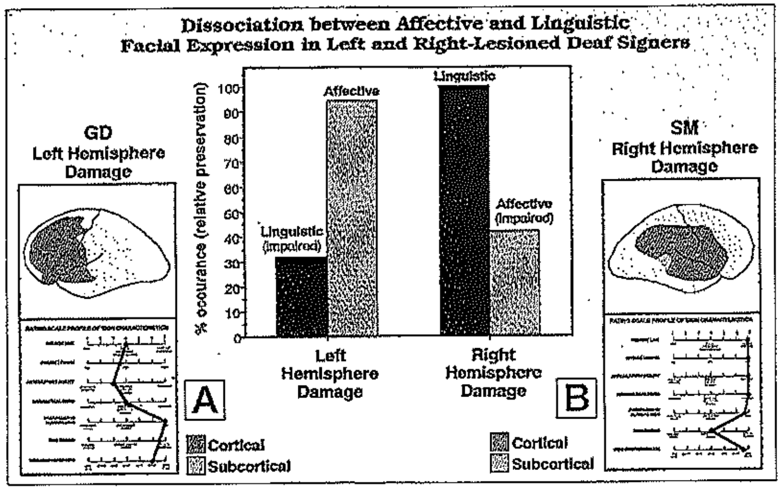
block design task. Note the RHD signers' tendencies to break the overall configuration of the design in the block design task and their spatial disorganization, compared to LHD. Yet, astonishingly, these sometimes severe spatial deficits among RHD signers do not affect their competence in a spatially nested language, ASL.

The finding that sign aphasia follows left-hemisphere lesions but not right-hemisphere lesions provides a strong case for a

modality-independent *linguistic* basis for the left-hemisphere specialization for language. These data suggest the left hemisphere is biologically predisposed for language itself, independent of language modality. Thus, hearing and speech are not necessary for the development of hemisphere specialization—sound is not crucial. Furthermore, the finding of a dissociation between competence in a spatial language and competence in nonlinguistic spatial cognition demonstrates that the type of information encoded in a signal (i.e., linguistic vs. spatial information) rather than the nature of the signal itself (i.e., spatial vs. temporal) determines the organization of the brain for higher cognitive functions.

Sign Language has been found to be preserved in right-lesioned signers. Signers with right hemisphere damage present special issues, since they often show nonlanguage spatial deficits. Several right-lesioned signers have severe left hemispatial neglect—that is, selective inattention to the left side of space, which is apparent in drawings, where the left side is frequently omitted. Or, in a task where they are asked to cross out all the lines on a page, they characteristically omit several lines on the left side of space (figure 4). The left-field neglect shows up on almost all visual tasks. Such a distortion in spatial cognitive abilities might certainly be expected to impact processing and production of a visual spatial language. Remarkably, this does not have an impact on signing or on the ability to understand signing, which is unimpaired. Inattention to the left portion of the visual field *does not hold* for linguistic stimuli.

In one experiment, we contrasted presentation of signs with presentation of objects to both visual fields. The sign trials used bimanual signs which have one meaning if information from both hands is processed but have a different meaning if information from only one hand is taken into account. The object trials involved simultaneous presentation of different objects in the two visual fields presented in the same spatial relations as the signs. The subject was nearly perfect on the sign identification task, but only half of the object trials were correctly identified, with all the errors involving omission of the object in left hemispace. This pattern of left hemispace omission was not observed in the sign trials. Moreover, although the drawings show left neglect, the subject used the left side as well as the right in producing signs and even used the left side of signing space for establishing nominals and verb agreement appropriately in sign language syntax (figure 4). These results show what little effect right hemisphere damage can have on core linguistic functions, even when the language is essentially visuospatial.



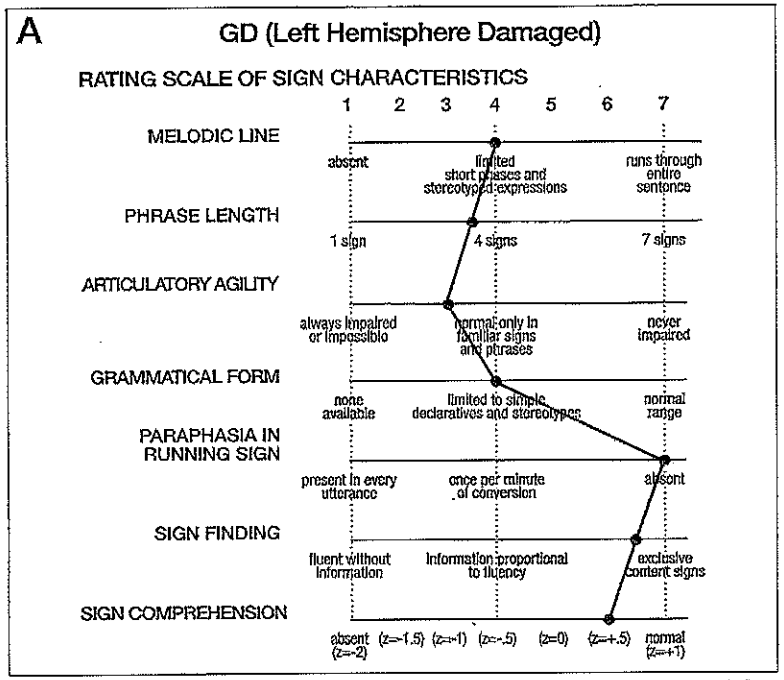
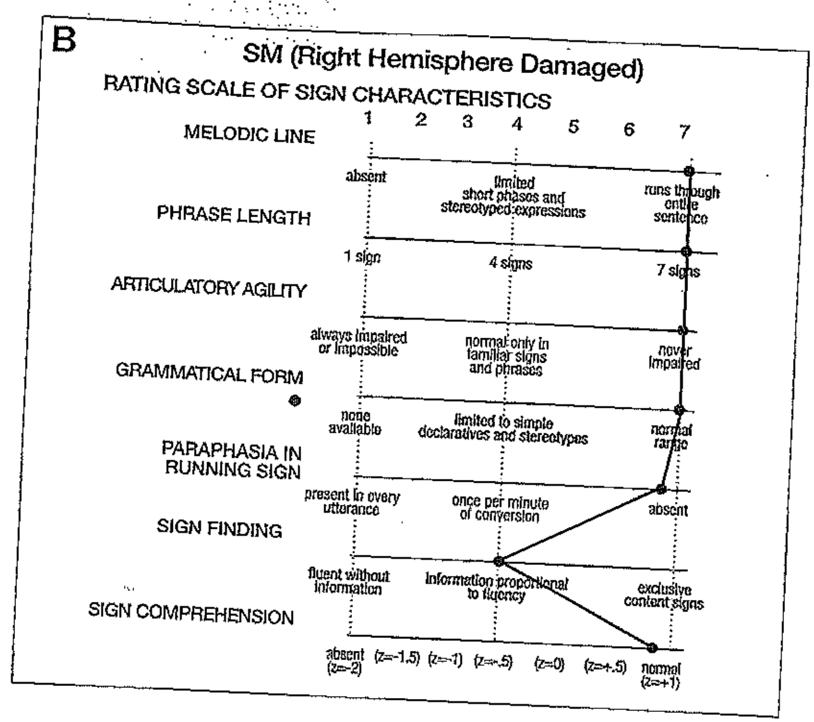


Figure 5. The dissociation between linguistic and affective facial expression in left- and right-lesioned deaf signers.



The Separation between Sign Aphasia and Apraxia

In a long-standing controversy over the nature of aphasic disorders, certain investigators have proposed a common underlying basis for disorders of gesture and disorders of language. One position is that disorders of language occur as a result of more primary disorders of movement control (apraxia). A second position is that both apraxia and aphasia result from an underlying deficit in the capacity to express and comprehend symbols. Since gesture and linguistic symbols are transmitted in the same modality in sign language, the breakdown of the two can be compared directly. In addition to an array of language tests, a series of apraxia tests was administered to brain-damaged deaf subjects, including tests of production and imitation of representational and nonrepresentational movements. The right-hemisphere damaged signers were neither aphasic nor apraxic.

Some strong dissociations emerged, however, between the language and nonlanguage gesture and motor capacities of the left-hemisphere damaged signers, most of whom were aphasic for sign language. The language deficits of these signers, on the whole, were related to specific linguistic components of sign language rather than to an underlying motor disorder. Nor were their language deficits related to an underlying disorder in the capacity to express and comprehend symbols of any kind. Indeed, we found a dissociation in a left-lesioned signer in the expression and the recognition of signs (which were impaired) contrasted with the expression and the recognition of symbolic gestures and mime (which were preserved).

Converging evidence comes from a study of signers and nonsigners without brain damage in which we compared lateralization for three different types of gestures: signs of ASL, symbolic gestures that are not part of a linguistic system, and arbitrary nonlinguistic gestures. Our results indicate left-hemisphere specialization for both sign and speech in hearing signers, and for sign in deaf signers, but not for arbitrary or symbolic gestures in either group. Thus, we find distinctions between motoric, symbolic, and linguistic communication in signers.

Affective and Linguistic Facial Expressions

Investigation of brain organization for sign language has focused primarily on the manual signs. However, there is another layer of structure of sign language that can afford special clues to the basis of hemispheric specialization, namely facial expressions. In ASL, facial signals function in two distinct ways: (1) Specific facial expressions have arisen as a part of the grammar, co-occurring with manual signs, and are used to signal grammatical constructions such as relative clauses, conditionals, topics, and so forth, and (2) for signers facial expressions can convey affective information just as facial expressions typically do with hearing non-signers.

Generally, studies of hearing subjects have shown that affective facial expression is mediated by the right hemisphere, but our research with deaf signers suggests that not all facial expressions are treated alike by the brain. Interestingly, we have found dissociations between left- and right-lesioned signers in terms of production of the two different functions of facial expressions. A right-lesioned signer was far more likely to produce linguistic facial expressions where required but showed a clear tendency to omit affective facial expression where expected. In contrast, two left-lesioned signers, who are aphasic for sign language but still produce complex ASL sentences, showed precisely the opposite effect, with full use of affective facial expression present throughout, but with frequent omissions of linguistic facial expressions where required

frequent omissions of linguistic facial expressions where required (figure 5).

These are important findings, since presumably one and the same muscular system is involved. Thus, one cannot account for the findings in terms of weakness of facial muscles but rather must account for them in terms of dissociation between linguistic and affective facial expressions. Like the processing of spatial relations, the brain basis for processing facial signals appears highly dependent on the type of information encoded in the signal. Linguistic facial signals are mediated by the left hemisphere, whereas affective facial signals are mediated by the right hemisphere in these deaf signers.

These results show that linguistic information and nonlinguistic information are mediated in qualitatively distinct ways in the brains of deaf signers. Not only does this cleavage show up in processing linguistic versus nonlinguistic spatial relations but also in perceptual attention and production of two different classes of facial expressions.

Spatial Syntax versus Spatial Mapping in ASL

Until now, we have considered the spatial organization underlying grammatical contrasts, most notably syntax, in ASL. That is, ASL uses spatial relations to encode syntactic information such as grammatical subjects and objects of verbs, through manipulation of arbitrary loci and relations among loci in a plane of signing space. As opposed to its syntactic use, space in ASL functions in a topographic way. The same plane of signing space also may be used in spatial mapping; that is, the space within which signs are articulated can be used to describe the layout of objects in space. In such mapping, spatial relations among signs correspond topographically to actual spatial relations among the objects described, as opposed to representing arbitrary grammatical information. We investigate the breakdown of two uses of space within sign language, one for spatially organized syntax and the other for directly representing spatial relations in ASL. Right- and left-lesioned deaf signers provide striking dissociations between processing spatial syntax versus spatial mapping. These subjects were given tests designed to probe their competence in ASL spatial syntax and spatial topographic processing. The combined results on the spatial syntax tests reveal significant differences between the two groups: left-lesioned signers were significantly impaired on syntax tests, but right-lesioned signers' performance was not distinguishable from normal controls. Contrastingly, on the tests of spatial topographic processing, right-

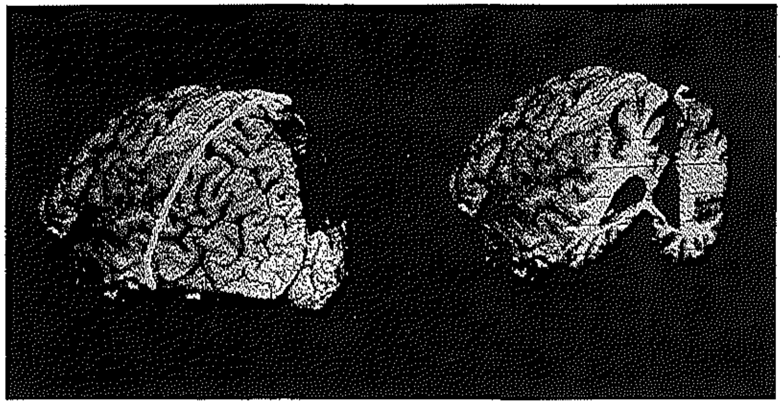


Figure 6. RHD lesion reconstructed by Brainvox (Damasio and Frank, 1992, courtesy of A. and H. Damasio).

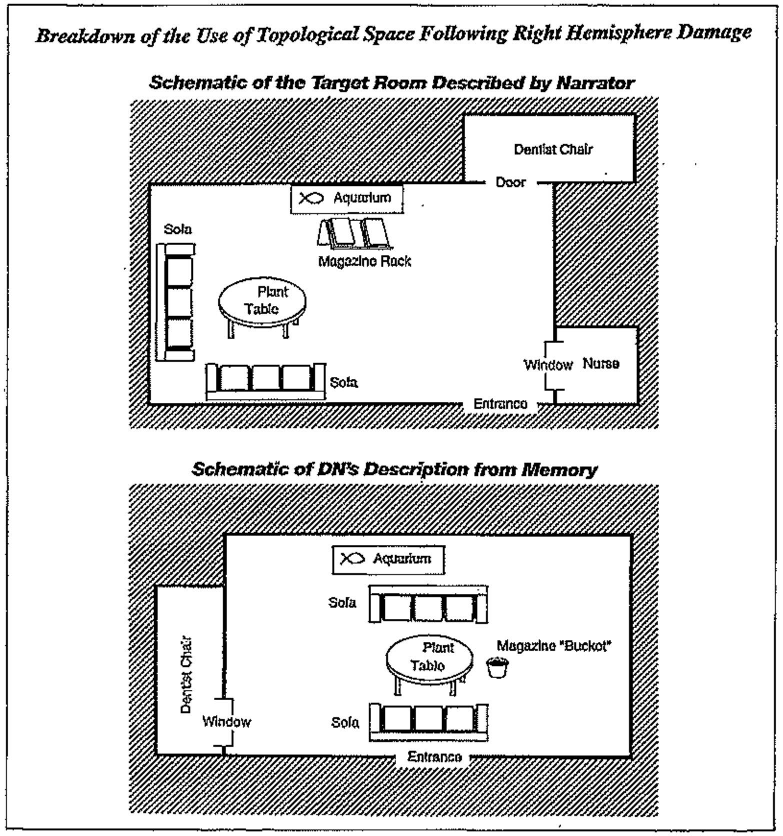


Figure 7. Disorganization in spatial mapping in right-lesioned signer.

lesioned signers revealed significant deficits, whereas left-lesioned signers performed well.

A powerful example of the dissociability of spatial syntax from spatial mapping comes from a RHD signer. The lesion of this subject involves the right superior parietal cortex with medial extension to the corpus callosum. This is illustrated in a three-dimensional reconstruction from in vivo MRI images using Brainvox, a system developed by Damasio and Frank (figure 6). Like other right-lesioned signers, the subject is not aphasic. Her processing on ASL grammar tests was nearly perfect, and her use of spatially organized syntax is error free. When she was asked, however, to repeat short stories in ASL that involved spatial descriptions—stories describing the layout of a particular dentist's office, for example—the description was impaired severely. This right-lesioned signer does quite well in remembering and reproducing the actual items within a description (unlike some of our normal controls), but she completely fails in placing these objects in correct spatial locations in the signed story. Control subjects correctly located nearly all the items remembered from the story, whereas our subject correctly located only about a third of the items remembered. The reconstructed layout of the signed description of a dentist's office is illustrated in comparison to the ASL description in the experiment in figure 7. This signed description shows a marked spatial disorganization of elements within the room; the subject incorrectly specified the orientation and locations of items of furniture but tended to lump all of the furniture in the center of the room, thus showing marked impairment in spatial mapping in ASL. Thus, even within signing, the use of space to represent *syntactic* relations and the use of space to represent *spatial* relations may be differentially affected by brain damage, with the syntactic relations disrupted by left-hemisphere damage and the spatial relations disrupted by right-hemisphere damage.

Converging Evidence about Brain Organization for ASL

A recent study by Damasio et al. analyzed the sign language of a hearing signer proficient in ASL during a left intracarotid injection of sodium amytal (WADA Test), and before and after a right temporal lobectomy for her epilepsy. Neuropsychological and anatomical asymmetries suggested left cerebral dominance for auditory-based language. Single photon emission tomography revealed lateralized activity of the left Broca's and Wernicke's areas for spoken language (figure 8). The WADA Test, during which all left lan-

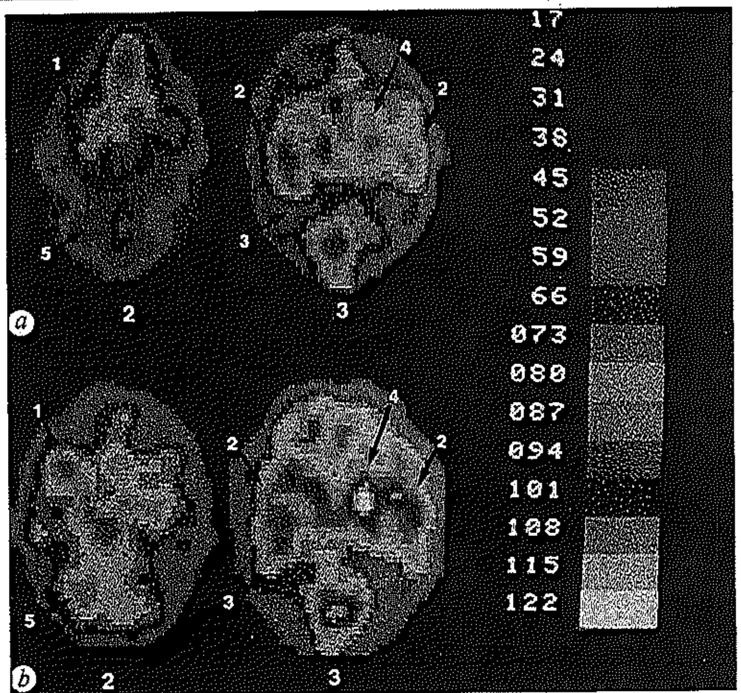


Figure 8. Single photon emission tomography reveals activity of the left Broca's and Wernicke's areas.

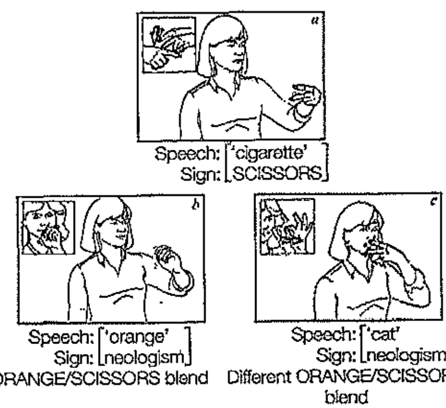


Figure 9. The conflict between Sign and speech errors during left WADA Test. (From *Nature,* reprinted with permission in TINS, courtesy of A. Damasio.)

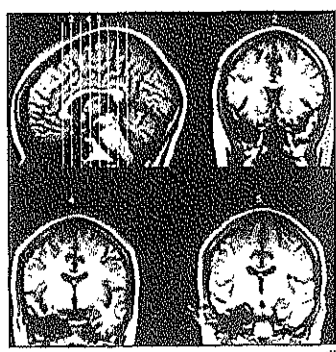


Figure 10. After surgery, English and sign language abilities are intact.

guage areas were rendered inoperative, caused a marked aphasia in both English and ASL. The patient's signing was markedly impaired, with many incorrect sign responses and sign neologisms. Interestingly, since she was hearing and could sign and speak at the same time, it was possible to compare her responses in two languages simultaneously—a unique possibility for languages in different modalities. This result revealed a frequent mismatch between word and sign, the sign being frequently incorrect both in meaning and in form (figure 9). Subsequently, the patient had the anterior portion of her right temporal lobe surgically removed (figure 10). Analysis of her language after the surgery revealed no impairment of either English or sign language. These findings further support the notion that the left cerebral hemisphere subserves language in a visuospatial as well as an auditory mode.

Techniques using cortical stimulation mapping and single-unit recording in a hearing signer, in a collaborative study with Ojemann, provide converging evidence. This approach allows us to contrast spoken and signed language neural systems within the same individual. During a left frontotemporoparietal craniotomy under local anesthesia, the subject was tested for both language modalities. The results showed some sites which differentiated sign from spoken word naming and comprehension. Single unit activity also was recorded, results suggesting that in this individual some sites representing sign versus word may turn out to be *different within* the left hemisphere. These converging results, taken together, provide strong evidence for the linguistic specificity of left-hemisphere specialization for language. The evidence so far does *not* suggest that the neural systems subserving the two languages will turn out to be precisely the same.

We are investigating differences as well as similarities between the neural systems subserving signed versus spoken language. Our growing database of deaf and hearing signers, combined with powerful new techniques in brain imaging, allows us to explore *within* the cerebral hemisphere neural systems subserving signed and spoken language. We now are beginning to amass evidence that suggests both some central commonalties and some peripheral differences between the neural systems underlying signed and spoken languages. Patterns of language breakdown and preservation in left- as opposed to right-lesioned signers lead us to the following conclusions: Because the left-lesioned signers show frank sign language aphasias and the right-lesioned signers show preserved language function, it appears that the left cerebral hemisphere is specialized for sign language. Thus, neural systems within the left hemisphere emerge as special-purpose linguistic processors in individuals with profound and lifelong auditory deprivation and who communicate with linguistic systems that use radically different channels of reception and transmission from that of speech. In this crucial respect, brain organization for language in deaf signers parallels that in hearing, speaking individuals.

Our data further suggest that differential damage within the left hemisphere produces different forms of sign language aphasia. We are working on the possibility that anatomical structures within the left hemisphere that subserve visual-gestural language differ in part from those that subserve auditory-vocal language. We now are mapping out the differences between spoken and signed language neural systems within the left hemisphere which may arise from the nature of the different visual input pathways and manual output pathways. Several left-lesioned signers exhibit sign language aphasias from lesions to systems that would not be expected to lead to language disruption in spoken language.

Language, Modality, and the Brain

Nonetheless, the similarities between signed and spoken language in interhemispheric organization are most revealing. These studies of language in a different modality show that the left cerebral hemisphere in humans is specialized for signed as well as spoken languages. Not only does this finding provide a striking example of neuronal plasticity, but it also suggests an innate biological basis for that unique human capacity: language.

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Suggested Readings

Bellugi, U. 1980. The structuring of language: Clues from the similarities between signed and spoken language. In *Signed and Spoken Language: Biological Constraints on Linguistic Form*, ed. U. Bellugi and M. Studdert-Kennedy, 115–40. Dahlem Konferenzen. Weinheim/Deerfield Beach, Florida: Verlag Chemie.

Bellugi, U., H. Poizner, and E.S. Klima. 1989. Language, modality and the brain. *Trends in Neurosciences* 10:380–88.

Bellugi, U., H. Poizner, and E.S. Klima. 1990. Mapping brain function for language: Evidence from sign language. In *Signal and Sense: Local and Global Order in Perceptual Maps*, ed. G.M. Edelman, W.E. Gall, and W.M. Cowan, 521–43. New York: Wiley-Liss.

Corina, D., H. Poizner, U. Bellugi, T. Feinberg, D. Dowd, and L. O'Grady-Batch. 1992. Dissociation between linguistic and nonlinguistic gestural systems: A case for compositionality. *Brain and Language* 43, no.3:414–47.

Damasio, A., U. Bellugi, H. Damasio, H. Poizner, and J. Van Gilder. 1986. Sign language aphasia during left hemisphere amytal injection. *Nature* 322:363–65.

Damasio, H., and A.R. Damasio. 1989. *Lesion Analysis in Neuropsychology*. New York: Oxford University Press.

Damasio, H., and R. Frank. 1992. Three-dimensional in vivo mapping of brain lesions in humans. *Archives of Neurology* 49:137–43.

Emmorey, K., S.M. Kosslyn, and U. Bellugi. 1993. Visual imagery and visual-spatial language: Enhanced imagery abilities in deaf and hearing ASL signers. *Cognition* 46:139–81.

Klima, E.S., and U. Bellugi. 1979. *The Signs of Language*. Cambridge, Mass.: Harvard University Press. (Paperback reprint, 1988.)

Poizner, H., E.S. Klima, and U. Bellugi. 1987. *What the Hands Reveal about the Brain*. Cambridge, Mass.: MIT Press/Bradford Books. (Paperback reprint, 1990. German translation: *Was die Hande uber das Gehirn Verraten*, Hamburg: Signum-Verlag, 1990; Japanese translation, Tokyo: Shinyosha Press, in press.)