

Sign Language and the Brain: A Review

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How are signed languages processed by the brain? This review briefly outlines some basic principles of brain structure and function and the methodological principles and techniques that have been used to investigate this question. We then summarize a number of different studies exploring brain activity associated with sign language processing especially as compared to speech processing. We focus on lateralization: is signed language lateralized to the left hemisphere (LH) of native signers, just as spoken language is lateralized to the LH of native speakers, or could sign processing involve the right hemisphere to a greater extent than speech processing? Experiments that have addressed this question are described, and some problems in obtaining a clear answer are outlined.

In order to understand how the brain processes signed language, we need a reasonable road map of the brain—its general structure and the probable functions of different regions. The study of brain injury (lesions) has provided a well-established methodology for inferring relations of structure and function in the brain. The consequences of brain lesions depend on which part of the brain is damaged. For example, a person with damage to the front of the left side of the brain might be unable to speak. However, someone else, with damage to the back of the right side of the brain, might be able to produce structured language utter-

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ances but may have lost some spatial abilities and be unable to see more than one thing at a time. Patterns like this appear to be highly systematic over many individual patients. One straightforward inference is that, in most people, the front of the left side of the brain is required for producing language, whereas the back of the right half of the brain is needed for visuospatial processing. That is, these two functions are “localized” and cannot be readily undertaken by other regions. Since the mid-19 century, the likely relationships between particular brain regions and their functions have been inferred from descriptions of such systematic patterns of individual brain injuries. Such research has provided a basic map of the brain upon which subsequent research has built.

A Tour of the Brain

As in all vertebrates, the human brain consists of two near-identical hemispheres, reflected on each other. The gray cortex (*cortex* = crust in Latin) comprises minute and densely packed nerve cells, to a depth of 0.5–1 cm. The corded band that connects the two hemispheres comprises many tightly bunched white fibers. Such fibers can also be seen beneath the cortex and run out to the spinal cord. These are bundles of individual nerve axons that carry information between nerve cells. Long axon fibers are organized in bundles (Latin—*fascies/fasciculi*), like cables that carry electricity, TV, or telephone information under urban roads. The glossy white protective sheath of myelin insulates

the nerve axon, enabling fast and reliable transmission of the nerve impulse. So, a simple overview of the human brain shows it to comprise two hemispheres comprising two forms of neural material: gray matter in the cortex and white matter organized in fasciculi. Electrical currents on the surface of the brain can be detected by exposing the surface of the brain and laying an electrode directly onto it (deep electrode mapping). When this is done, voltage changes are observed, as activity spreads from one part of the cortex to its neighbors and along the insulated white “cables” to distant parts of the brain. These dynamic electrochemical changes can be considered to be a signature of brain activity corresponding to mental events and processes.

In human compared with other primate brains, the cortical surface has become deeply folded to accommodate a large increase in gray matter volume within the relatively small human skull. Increasing the complexity of the brain surface also means that different cortical regions may be connected in new ways. The

general pattern of folds and creases is systematic from person to person. Four main lobes make up each hemisphere: frontal, temporal, occipital, and parietal (see Figure 1). Within each lobe, further recognizable landmarks are made by distinctive ridges (Latin—*gyri*), folds, and creases (Latin—*sulci*) on the cortical surface (see Figure 1). Although Figure 1 is a very reduced map of the brain, showing only the outer left surface and undersurface, it should indicate the relative positions of the regions discussed in this paper.

Exploring the Brain—The First Discoveries About Language

Individual clinical case studies have been reported since antiquity (see Finger, 2001). However, the first discoveries about language and the brain were brought into the realm of systematic clinical research in the mid-19 century. The discovery that in hearing people lesions of the lower part of the lateral left frontal quadrant of the brain often give rise to difficulties in

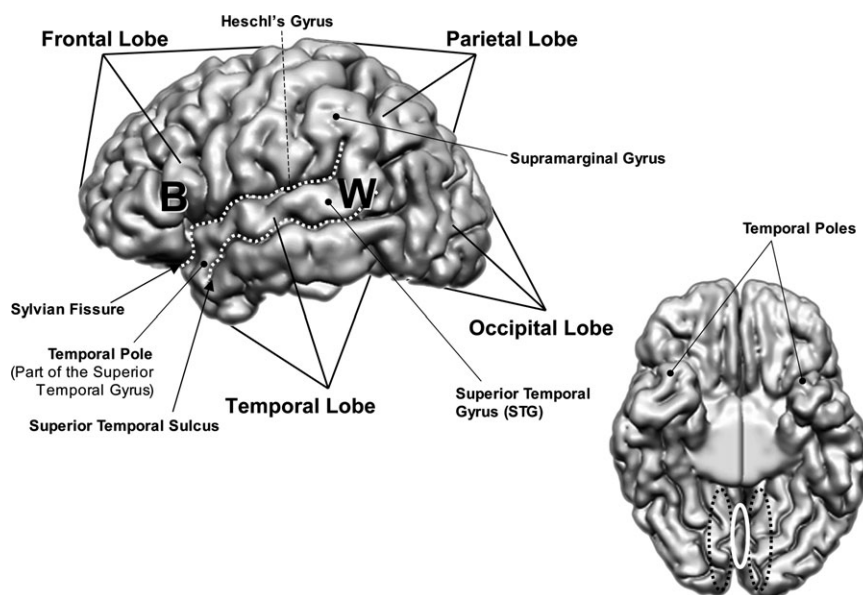


Figure 1 A diagrammatic lateral view of the LH and undersurface of the brain. The left lateral view (top left of figure) shows the four different lobes of the brain and some cortical landmarks for language processing. The front of the brain is at the left of the figure. Primary auditory cortex lies within Heschl's gyrus. This is hidden from view within the Sylvian fissure on the upper surface of the temporal lobe. Secondary auditory cortex includes surrounding superior temporal areas. The approximate locations of Broca's (marked with a "B") and Wernicke's (marked with a "W") areas are also shown. A view of the undersurface of the brain is also displayed (bottom right of figure). The front of the brain is at the top of this figure. The approximate locations of primary visual cortex (white oval) and secondary visual cortex (dotted black ovals), located at the back of the brain, deep within sulci in the occipital lobe, are indicated.

speaking has been credited to the French neurologist Paul Broca (1824–1880), after whom this part of the brain was named (see Figure 1). The problem with patients with lesions here is not just in articulation. A person with injuries to Broca's area may be able to utter a well-learned phrase perfectly ("Excuse me, please!"), but be unable to find or build up an appropriate phrase or word to describe what they want to say. Sometimes they may be unable to produce a word at all, especially if it is a function word, such as "the," "unless," or "if." Often, these patients can make their intentions and understanding clear by gesture: they may nod (yes) or shake their head (no) correctly in response to questions and can sometimes use their left hand (control of the right hand is also affected by damage to prefrontal regions of the left hemisphere [LH]) to make an appropriate gesture or to write a word or two. This pattern suggests that although the inferior front (anterior) part of the LH may be critical for producing spoken language, and especially for building sentences, damage to this region does not destroy the individual's ability to communicate.

The production of speech requires the left frontal regions. The perception of speech, however, relies more on regions further back in the LH, within the temporal lobe. The role of the upper left temporal cortex in speech comprehension was established by the neurologist Carl Wernicke in the 1870s and this region of the brain was later named after him (see Figure 1). In contrast to patients with damage to the left frontal lobe, who have difficulties in producing speech but have relatively good comprehension (Broca's aphasics), patients with left-sided temporal damage (Wernicke's aphasics) can often speak fluently, but fail to understand speech (Cabeza & Kingstone, 2001). Wernicke's region appears to be specialized for the perception of speech sounds. It includes the upper (superior) parts of the lateral temporal lobe, extending from the middle of the superior temporal gyrus and its underparts (the superior temporal sulcus) backwards and upwards to the junction with the parietal lobe at the supramarginal gyrus (see Figure 1).

The Sylvian fissure is the fold that can be seen to separate frontal and temporal lobes. The cortex that surrounds it is referred to as "perisylvian." Both the upper part of the lateral temporal lobe (Wernicke's

area) and the lower lateral part of the frontal lobe (Broca's area) fall within perisylvian regions. By the middle of the 20th century, the left perisylvian regions were well established as critical language-processing regions for hearing, speaking people: but what of signed languages? We have noted that patients with damage to Broca's area can often gesture communicatively. Does this mean that a visual-gestural language may be unaffected, if there is brain damage to this region?

Brain Lesions in Signers

A pioneering series of case studies (Poizner, Klima, & Bellugi, 1987) gave a very clear answer to this question. These researchers reported six cases of unilateral stroke in deaf people who used American Sign Language (ASL) as their primary language. Those with damage to the LH had language problems. Damage to left frontal regions was associated with production difficulties in ASL (Broca's-like aphasia), whereas damage in the left temporal lobe was more likely to cause problems in comprehension of ASL (Wernicke's-like aphasia). Right hemisphere (RH) damage did not cause problems in linguistic aspects of perceiving or producing signed utterances. To date, around 30 patients with acquired brain damage, who use a signed language as their primary language, have been reported. The original finding that signed language was affected specifically by damage to the LH has been confirmed and supported for a small number of signed languages: ASL and British Sign Language (BSL) especially (see Corina, 1998; Hickok, Love-Geffen, & Klima, 2002; Marshall, Atkinson, Thacker, Woll, & Smulevitch, 2004).

Whether signed or spoken language is investigated, the location of brain damage seems to have remarkably similar (and specific) effects. The left perisylvian regions are critical for language function. Although they lie very close to auditory processing regions (see Figure 1), language processing is not determined by the auditory input modality. These pioneering findings helped to establish the modern conceptualization of signed languages as "real languages," as valid for linguistic inquiry as spoken languages. The hidden argument here is that because

both spoken and signed languages appear to depend on the same cortical substrate, they may be considered functionally equivalent in terms of their cognitive and linguistic bases. This is not a watertight inference, but it has served as a good heuristic for exploring the cortical bases of signed languages.

Although the lesion studies seem conclusive, nevertheless there is a lingering suspicion that signed language processing may require the contribution of the RH to a greater extent than languages that are spoken. Studies of spoken languages suggest that the RH is specialized for many functions vital to language. These include how descriptions of events link to each other from sentence to sentence (discourse cohesion) and the “melody” of a phrase or series of phrases, which varies depending on what aspect is being communicated (*prosody*: the pattern of spoken intonation and stress—see Beeman & Chiarello, 1998). The RH appears to support these functions in signed languages, too (Hickok et al., 1999). However, some researchers suspect that signed language may engage the RH to an even greater extent than spoken language. There are a number of reasons for this, which derive from a wealth of studies of hearing people who use spoken languages.

1. The RH is dominant for a range of visuospatial processing abilities (Hellige, 1993). Earlier theorists (e.g., Witelson, 1987) had suggested that the LH is specialized for sequential processing and the right for simultaneous processing. From this it is easy to infer that speech, which cannot use space as a linguistic feature and must use time-varying signal change to encode language, must be LH specialized. Signed language, which can use space to encode language, may enjoy more RH processing. However, it would be a mistake to believe that signed languages are exclusively spatial and nonsequential in their linguistic structures (Liddell & Johnson, 1989; Sandler, 2006). Furthermore, we must be careful of conceptualizing left–right differences as left–sequential and right–spatial. For example, the RH, rather than being relatively poor at processing visual movement (a time-based, sequential skill), can be more proficient than the LH at detecting and interpreting visual movement (Grossman et al., 2000). A more appropriate concep-

tualization of the relative strength of the RH may be that it shows a marked specialization for discriminating the shape, size, and configuration of a visual object; its position in space; and some aspects of its movement. We might expect this to contribute to the analysis of signed language to a greater extent than it does to spoken language.

2. A widely held idea about the relative strengths of LH and RH is in terms of “grain” of processing units. The LH is often better at perceptual processing of fine-grained inputs. It responds best to visual displays of high spatial frequency, with fine visual detail, and to fast rather than slow-changing moving stimuli in auditory or touch input. Production, too, may follow similar principles. The LH is dominant for planning finely articulated actions in speech and for finger rather than hand positioning in imitating manual actions (Goldenberg & Strauss, 2002). By contrast, the RH is specialized for “coarse-grained,” global aspects of the stimulus material such as the perception of high-contrast patterns or the larger shape in a figure made up of smaller ones. Perhaps signed languages make use of relatively more “holistic” actions to represent linguistic entities than do spoken ones.

3. The RH is dominant in social communication—including judgment of appropriateness of social acts and pragmatic aspects of communication (see Winner, Brownell, Happé, Blum, & Pincus, 1998). It is dominant for the processing of faces (Sergent, Ohta, & MacDonald, 1992) and many facial acts, including decoding of emotional expression (Davidson, Shackman, & Maxwell, 2004). The perception of body movements and positions also shows marked RH specialization (Meador, Loring, Feinberg, Lee, & Nichols, 2000).

It is entirely possible that these distinct specializations may be involved in sign to a greater extent than they are in speech. However, when we seek a specifically “linguistic” contribution of the RH to language processing in lesion patients, it is remarkably difficult to find one. One RH-lesioned patient, D.N., who was a user of ASL, showed some highly specific difficulties in understanding signed language. However, it can be argued that, even for this patient, it was spatial rather than linguistic complexity that determined her difficulties (for discussion, see Emmorey,

2002). This question remains open to investigation however, and more detailed studies of the differential effects of unilateral lesions should help to clarify this issue.

Interpreting Lesion Studies

The findings of Poizner's team and of subsequent studies of brain-lesioned patients are not the last word in understanding the localization of signed languages in the brain. An eminent British neurologist noted: "To locate the damage which destroys speech and to locate speech are two different things" (Jackson, 1864, cited in Head, 1926, p. 50). Lesion studies indicate brain regions that are critical for the performance of a particular task but cannot show all of those that are actually engaged. In the damaged brain of a person with aphasia, regions which may normally be active during that task may still function—but their contribution may be silent because they send input to a critical lesion site. An analogy would be the effect of a traffic holdup on a motorway. From a point beyond the holdup, we cannot tell whether the absence of traffic is due to a local blockage or if there just is no traffic coming from a distant region. Moreover, because activity in some brain regions may inhibit the actions of others, lesions can lead to masking of normally occurring processes—or even release some functions that would normally be suppressed (paradoxical facilitation). On top of this, lesion studies give us a picture of how someone performs a task *after* localized damage has occurred. Compensatory processes may mask some effects of damage and conceal the role of different brain regions in normal functioning. All this means that some of the jigsaw pieces that have been used to build up the picture of how the brain functions might be out of place. Moreover, brain lesions are accidents of nature. Not all brain regions are susceptible to injury, and few brain injuries are confined to just one "region of interest." Thus, it is unlikely that all the jigsaw pieces will be available to obtain the full picture, if we rely on brain lesions alone.

Brain Plasticity—Lifetime Events Can Affect the Brain

Another set of factors that need to be considered in relation to how the brain develops localized special-

izations is the environment to which an individual is exposed during their lifetime. Although the discussion so far has drawn a picture of the brain that seems to be consistent from person to person, nevertheless, a range of cultural and environmental factors impact on brain development, causing individual differences in patterns of brain localization. These are becoming clearer as brain activation patterns are probed using neuroimaging techniques (see below). Prelingual deafness and adjustment to the early loss of hearing might set some brain processes along a different developmental track than those for hearing people (Bavelier, Dye, & Hauser, 2006; Bavelier & Neville, 2002). If deaf brains may differ from hearing brains from the outset, then the localization of signed language processing may depend on the hearing status of the user (see below). Events later in life can affect brain development too. Hearing people who are literate show different patterns of brain activation than those who have not been schooled to read and write (Petersson, Reis, Askelof, Castro-Caldas, & Ingvar, 2000). Chinese people who learn a nonalphabetic language show distinctive activation in brain regions that recognize letterforms, compared with people whose written language is alphabetic (Siok, Perfetti, Jin, & Tan, 2004). Bilingual people can show different brain organization than monolinguals (Mechelli et al., 2004). A study with hearing people showed differences in brain activation between early and late learners of ASL while they watched signed sentences (Newman, Bavelier, Corina, Jezzard, & Neville, 2002). Such findings suggest that brain activation patterns are highly sensitive to a range of factors such as literacy, orthography, age of language acquisition, and the conditions of second language learning in the context of a previously learned language. They should lead us to examine carefully the language culture of the people who are the source of our information about brain specialization. Are we seeing in them examples of general principles at work about deaf brains and signed language? Or are we seeing an individual variant of those principles, reflecting the individual's particular background? Is our participant a deaf person from many generations of a Deaf family, or is she a signer who learned to sign only in later childhood—perhaps at a Deaf school? How might the deaf person's literacy affect the

functional organization of their brain for other language skills? These questions are only now starting to be addressed, and we will return to them later in this review.

Beyond Brain Lesion Studies—Neuroimaging in the 21st Century

Considerations such as those mentioned above come to the fore when we consider more recent approaches to the question: how is a signed language processed in the brain? These newer approaches allow us to see in some detail how the normal brain functions, so we do not have to wait on accidents of nature to produce brain lesions. Since around 1980, such methods have become increasingly available. These newer studies may extend our understanding beyond that available from the classical lesion studies. Taking on board the comments in the previous section, we should now be alert to the possibility that different participant groups, who may have different sorts of exposure to and use of sign, may show distinctive activation patterns. Moreover, direct measures of healthy brain function can help counter some of the shortcomings of the lesion approach. They ought to be able to show us the function of different regions of the brain for which we do not have lesion evidence. Where lesion evidence and neuroimaging evidence coincide, we can have more confidence that that part of the jigsaw puzzle is a proper fit. Observing the healthy brain at work not only should help us identify those regions that are critical to the performance of a language task but also, if we design our studies properly, can show us the regions and patterns of activity that feed into that task (see Price, 2000, for further discussion). A number of relatively noninvasive methods are currently used to explore language function in the healthy human brain.

Electrophysiological Methods

One way neurons communicate is by using electrical energy. A region that is neurally active is therefore electrically active. Although this activity occurs within the brain, some of it can be measured on the surface of the scalp by mapping local electrical field changes (electroencephalography, EEG). From these measurements, inferences can be made about where and when

the activity occurred “below the surface.” Specific cognitive events carry distinct EEG signatures. These are event-related potentials (ERPs). ERPs can provide millisecond resolution of the neural activity associated with a specific event, so inferences can be made about the speed and time course of processing across the brain (see Picton et al., 2000, for an overview).

Here is one way this method has been used to explore language processing. People are fitted with a hairnet or elastic cap equipped with EEG sensors, which lies comfortably on the scalp. They read, watch, or listen to a phrase which may contain an anomaly, such as “I like my coffee with cream and *dog.” A specific brain event occurs when a word appears that does not fit the meaning of the sentence. Evidence of this can be seen in the EEG trace, and it occurs before a behavioral response (such as saying “what did you say?” or pressing a button) can be observed. One such “anomaly detection response” is a negative-going (N) waveform occurring 400 ms after the critical word was shown. This N400 waveform is seen over both sides of the brain and is greatest in middle-posterior regions. When a different sort of written sentence anomaly is presented, one where the anomaly is syntactic—for instance, an inappropriate function word (“I went to the shops and my mother came *it”), a different and earlier negative waveform occurs. This happens about 280 ms after the critical point in the sentence (N280 waveform). It localizes to the front of the brain and is confined to the LH (Neville, Mills, & Lawson, 1992). These different waveforms may be considered to be markers for semantic processing (N400, middle regions, bilateral) and for online syntactic processing (a left anterior negativity, or LAN). This could be construed as further evidence that the LH is dominant for language processing because it is widely argued that syntax is the essential property of language, whereas the understanding of meaning may rely on additional knowledge and processing that makes use of both hemispheres. The slightly different time course and spatial distribution of each waveform suggests that semantic and syntactic processing recruit different regions of the brain at different points in time—suggesting separable processing systems. Some syntactic elements can be processed quickly, predominantly in the LH, while a sentence is being shown.

Semantic changes in a phrase or sentence may tend to require somewhat slower, more integrative processing. These may involve additional brain regions to those in left perisylvian regions—in particular, middle regions of the temporal lobes, in both the LH and the RH. These patterns not only occur for written but also for spoken sentences (see Friederici, 2004, for an overview).

The ERP technique has been available to researchers for over 30 years, but has been applied to signed language comprehension in only a handful of studies, pioneered by Helen Neville et al. (1992,1997). Neville et al. (1992) explored ASL sentence processing in deaf native signers and compared their findings to their earlier study of hearing speakers reading English. The waveform thought to reflect semantic processing (N400) showed a similar time course and distribution for both ASL processing in deaf signers and reading English in hearing nonsigners. However, responses to function signs (closed-class signs) were bilateral rather than left sided in deaf participants. Because closed-class items are associated with syntactic (as opposed to semantic) processing, this suggested that the processing of some syntax-related elements in ASL might involve both RH and LH, rather than the left-localized activation observed for hearing nonsigners reading English. It suggests that perhaps syntactic processing for ASL is not as completely left-lateralized as it is for English. More recent ERP studies supported this conclusion. One class of verbs (termed “agreement verbs”) in signed languages show syntactic agreement when the direction of manual action is toward the referent (Padden, 1988; but see Liddell, 2000). Capek et al. (2001) showed deaf native signers’ ASL sentences in which the verb was reversed in direction (i.e., was syntactically wrong). They found an early anterior negativity that was larger over the LH (i.e., a LAN), similar to that seen in hearing people reading or listening to syntactic anomalies in sentences. However, verb agreement violations in which the verb was directed to a new location (instead of toward the already defined referent), elicited a bilateral anterior negativity. So it seems that the type of syntactic element being processed, in this case the direction and movement of the action term, can affect the electrophysiological trace and that under certain syntactic

anomaly conditions, a LAN can be observed for sign processing in just the same way as it had been observed for speech. The conditions under which the RH is involved may reflect the demands of spatial syntactic processing, that is, they may be specific to signed languages. However, we do not yet know whether there are analogues of this type of bilateral early negativity that could occur in speech processing: they simply have not been sought. This is a good example of how research on signed language can generate hypotheses for spoken language and not only vice versa. For the present, because similar LH regions may be dominant for at least some syntactic violations both in (native) sign and English perception, it is safe to conclude that both signed and spoken languages utilize left perisylvian regions for syntactic processing. The most important thing to note is that the main conclusion drawn by Neville and colleagues from these studies was that syntactic processing in sign can also involve the RH, and in this respect sign may reflect bilateral processing specializations to a greater extent than does speech. We return to this possibility below.

Positron Emission Tomography and Functional Magnetic Resonance Imaging Studies of Sign and Speech

ERP methodology has very good temporal resolution, but relatively poor spatial resolution. ERPs will not get us much beyond right or left, front or back, or upper or lower regions of the brain. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) are two methods that offer a clearer view of the cortical locations that are active during mental tasks, and it is to these that we now turn. They both work on the principle that when a region of the brain is engaged in a specific task, an increase in blood supply is needed to provide oxygen to sustain the increase in neural activity. Usually, this happens a few seconds or so *after* the neural activity has started, so these techniques offer, at best, only an indirect view of the timing and order of cortical events. PET and fMRI measure this blood flow in slightly different ways. In PET, the first of the two methods to be developed, a radioactively labeled substance such as oxygen is introduced into the bloodstream. This labeled oxygen

then accumulates in the parts of the brain that are active. When the radioactive material breaks down, a neutron and a positron are emitted. When a positron collides with an electron, both are destroyed and two gamma rays are released. The location of this event is then detected by the PET camera.

fMRI capitalizes on the magnetic properties of the blood. An iron-based carrier molecule in blood (hemoglobin) enables oxygen to be delivered to different organs of the body. Whenever a particular body function (including neural excitation) uses oxygen from the blood (oxygen metabolism), the hemoglobin molecule changes form and a local magnetic field is established, which has different characteristics than when oxygen has not yet been taken up by the tissues. Changes in this extremely weak magnetic field can then be identified using a magnetic resonance scanner. The scanner produces a strong magnetic signal that interacts with the small local magnetic field changes induced by the brain activity. From this, we infer the regions that have been most active during a particular task. fMRI does not require injection (which is usually required for PET), but because the volunteer is surrounded by the strong magnet when being scanned, participants must have no ferrous metal in their body (thus ruling out, e.g., volunteers with cochlear implants). The experience is also noisy and claustrophobic.

Both PET and fMRI indicate regions of increased neural activity by measuring, albeit indirectly, blood flow changes in the brain. Because blood is constantly flowing through the brain, there is no natural resting level that can be measured. This means that one cannot gain a picture of the regions that are activated by signed language processing alone, but regions activated by signed language compared with regions activated by another task. When you read that signed language processing resulted in increased activation in areas X and Y in the brain, the first question must be—in contrast to what?

Brain Structure—Do Deaf and Hearing Brains Differ?

Magnetic resonance methods can be used not only to gain images of brain activity (function) but also can inform about the size and shape of gray and white

matter within individual brains (structure). The first question must therefore be: do deaf people's brains look different than those of people who can hear? To date, only two studies have explored this critical question. In terms of the landmark regions of the brain (see Figure 1), the answer currently seems to be "No" (Emmorey, Allen, Bruss, Schenker, & Damasio, 2003; Penhune, Cismaru, Dorsaint-Pierre, Pettito, & Zatorre, 2003). There is no indication that (for instance) regions that support auditory processing in hearing people are of smaller volume in deaf people. However, subtle differences are apparent. For instance, one report suggests that the white matter connections between brain areas differ in deaf and hearing brains (Emmorey et al., 2003), with relatively thicker connections between auditory and perisylvian regions in hearing people. These studies are in their infancy, and improvements in technology will enable more sensitive measures to be made. For instance, gray matter density and the precise configuration of the white matter tracts that connect the different regions in deaf and hearing brains remain underexplored.

Brain Function—Do Sign and Speech Engage the Same Regions?

Even when brains look the same, different brain regions may function differently depending on a variety of factors. There are a number of ways to find out whether signed language makes use of identical brain systems to those used for spoken language, or whether they are different. In the first place, people who have access to both speech and sign can be investigated. Signed and spoken language can be directly compared in these bilinguals. Using PET, Söderfeldt, Rönnerberg, & Risberg (1994) and Söderfeldt et al. (1997) contrasted Swedish Sign Language (SSL) and audiovisual spoken Swedish in hearing native signers. Whereas the first study found no significant differences between the two language inputs, the latter study, using more sensitive image analysis and a more complex design, found differences as a function of language modality. However, these were not in perisylvian language regions, but in the regions that are specialized for different input modalities. Auditory cortex in the superior temporal lobe was activated more by spoken language, whereas parts

of visual cortex (posterior and inferior temporal, and occipital regions) were activated more by signed language. But these may be a special population: hearing people who have had extensive experience not only with SSL but also with spoken and written Swedish. Could the fact that these participants were bilingual in sign and speech have driven the pattern observed? Perhaps these findings only apply to hearing native signers while deaf native signers may show differences from the spoken language pattern? We have already noted that lifetime events, such as exposure to different types of language and whether one or several languages are mastered, can affect patterns of localization in hearing people when other languages than signed languages are considered.

Neville et al. (1998; see also Bavelier et al., 1998) used fMRI to examine deaf and hearing native signers of ASL. Activation as participants watched video displays of ASL phrases was contrasted with activation as they watched nonsense gesture that had superficial similarities with ASL. Hearing English-speaking nonsigners were also tested. This group was presented with written sentences (shown one word at a time), contrasted with consonant letter strings. In order to check that participants were actively processing the material, they were required to remember what they had seen and were given a memory test at the end of the scan session. Reading English (hearing nonsigners) and watching ASL (deaf and hearing native signers) both activated classical language regions in the LH. These findings support the lesion data: the left perisylvian cortex is critical to language processing. However, in both deaf and hearing native signers there was also extensive activation in the RH, including the right perisylvian regions. On the basis of their previous ERP study (see above), Neville et al. (1998) argued that the involvement of the RH was most likely due to the increased spatial processing demands of grammar in ASL. The authors summarized this difference as “left invariance, right variability” (Bavelier et al., 1998). This phrase was used to capture the finding that in addition to the recruitment of classical left-lateralized language areas, signed language processing in native ASL signers appeared to recruit the RH to a greater extent than written language processing in hearing nonsigners. This conclusion has generated

much comment because it does not fit well with the aphasia studies. If the RH were needed for sign processing, then patients with right-sided or bilateral lesions might be expected to have some difficulties signing while people with LH lesions should not show such severe sign-processing problems. The main criticism centered on whether the contrast between ASL and written English was valid (Corina, Bavelier, & Neville, 1998; Hickok, Bellugi, & Klima, 1998; Paulesu & Mehler, 1998). The written English sentences were shown one word at a time, lacking the intonation, stress, or other prosodic features typical of face-to-face communication. In contrast, the ASL sentences were presented naturally, with their normal discourse properties. Prosodic features, used to interpret the discourse meanings of an utterance, can activate right-lateralized regions in neuroimaging studies of spoken language (Friederici & Alter, 2004), and patients with RH lesions often have difficulty with such features, in both sign and speech (Hickok et al., 1999). In addition, signers were presented with their native language in its primary form. In contrast, written English is learned as a secondary language form by hearing people, building on the individual’s knowledge of the spoken language. These differences, rather than any intrinsic characteristics of speech and sign, may have led to the conclusion that signed language might activate the RH more than reading.

Signed Language Versus Audiovisual (Natural) Speech

To address some of these concerns, MacSweeney et al. (2002b) compared BSL presented to deaf native signers with audiovisual English presented to hearing monolinguals. The perception of BSL and audiovisual English sentences recruited very similar neural systems in native users of those languages. As in the study by Neville et al., both languages recruited the perisylvian cortex in the LH. However, there was also RH recruitment by both languages and no differences in the extent of recruitment of the RH by the different language modes (see Figure 2a, columns 1 and 3). Presumably, this reflected the contribution of both hemispheres to comprehension of the sentences presented—whether the language was spoken or signed.

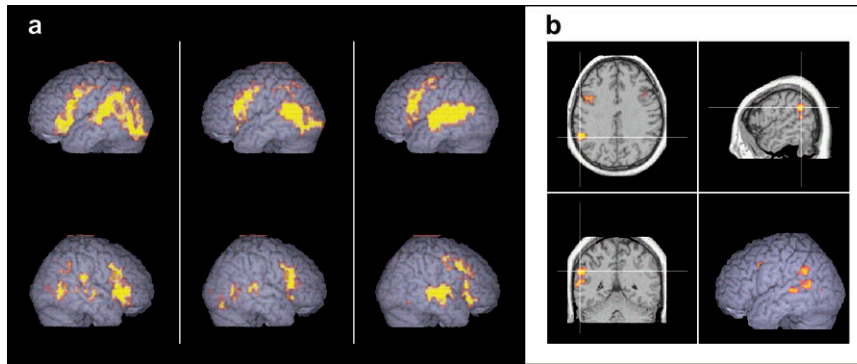


Figure 2 Color-rendered images of the brain depicting (group) fMRI activation. (a) Regions activated by BSL perception in deaf and hearing native signers (first and second columns, respectively) and by audiovisual speech perception in hearing nonsigners (third column). For language in both modalities, and across all three groups, activation is greater in the left than the right hemisphere and perisylvian regions are engaged (reprinted from MacSweeney et al. [2002a] with permission). (b) Colored regions are those recruited to a greater extent by BSL perception than TicTac (nonsense gesture) in deaf native signers. We interpret these regions as being particularly interested in language processing. Activation up to 5 mm below the cortical surface is displayed. Crosshairs are positioned at Talairach coordinates: $X = -58$, $Y = -48$, $Z = 31$. This is the junction of the inferior parietal lobule and the superior temporal gyrus (reprinted from MacSweeney et al. [2004] with permission).

It was argued by the authors that when like was compared with like, using face-to-face sentence-length utterances in both languages, then the neural systems engaged were very similar.

As predicted, some differences between the groups were observed that reflected the modality of input. Hearing people presented with a speaking model showed more activation in auditory cortex. Deaf people watching BSL recruited occipito-temporal regions specialized for visual processing to a greater extent. This pattern of difference echoes that found by Söderfeldt et al. (1997) for hearing native signers watching both SSL and speech. Taken together, this suggests that many of the differences between spoken and signed language patterns of activation reflect the modality-specific processing requirements of the perceptual task, rather than the linguistic aspects of it.

Homing in on Language-Specific Regions

Another perspective can be obtained by contrasting the processing of linguistically well-formed material with material that may be superficially similar but which cannot be analyzed linguistically (nonsense gesture). This type of contrast addresses the question: are the brain bases for signed language processing the same as those for the processing of other visual gestures? That is, are they specific to the processing of

linguistic gestures? In one study, MacSweeney and colleagues contrasted BSL utterances with gestures derived from TicTac. This is the gestural code used by racetrack bookmakers to signal betting odds to each other (MacSweeney et al., 2004). The stimuli were modeled by a deaf native signer who constructed “sentences” using hand gestures derived from TicTac codes, adding in appropriate nonmanual markers (facial gestures). Superficially, the displays of BSL and of TicTac-like gesture were similar, and both types of input caused extensive activation throughout both the left and the right superior temporal lobe when compared to watching the model at rest. That is, much of the upper part of the temporal lobe likes to watch gestural displays whether these are linguistically structured or not. However, the brains of the signers who viewed the displays discriminated between the inputs: BSL activated a particular left-sided region much more than TicTac. This is located at the junction of the left posterior superior temporal gyrus and the supramarginal gyrus in the parietal lobe (see Figure 2b). This difference was not due to perceptual differences in the visual quality of the stimuli because hearing people with no BSL knowledge showed no differences in activation between BSL and TicTac in this region. This very posterior part of Wernicke’s region appears to be particularly interested in signed language processing, just as it has been shown to be for

spoken language processing using similar experimental paradigms (see Scott, Blank, Rosen, & Wise, 2000; Narain et al., 2003). Thus, this appears to be a language-specific region that is not sensitive to the modality of the language it encounters.

The Puzzle Remains

Why do some studies find signed language perception to be lateralized to the LH while others, especially those involving deaf signers of ASL, report additional RH activation? Part of the answer may lie in the task differences: for instance, a memory task (Neville and colleagues) compared with anomalous sentence detection (MacSweeney and colleagues) may generate different strategies in the perceiver. These are known to affect brain localization. Also, different studies have used different comparison groups and modes of language presentation: signed language may be compared with written, spoken, or audiovisual speech. But other factors may also be important. Perhaps the ASL and BSL experiments have recruited from rather different populations. Although both groups were native signers, were both similarly bilingual in sign and speech? Could differing levels of literacy in spoken English have contributed to the different patterns? Do BSL and ASL contain as yet undetected grammatical differences that have generated these findings? This discrepancy between the studies of ASL and of BSL underlines the need for further studies, using a variety of different signed languages and also a variety of signers with different language experiences and backgrounds. The answer may be a simple experimental discrepancy or it may reveal a more interesting theoretical difference between the languages or populations tested.

Sign Production

Although questions have been raised regarding the contribution of the RH to signed language perception, the picture appears to be much clearer for production. Sign production is strongly left-lateralized, however assessed, and whatever language or language group is studied. Using PET, McGuire et al. (1997) asked deaf native signers of BSL to covertly sign sentences in response to a model producing a signed ad-

jective cue (e.g., cue: HEAVY; covert response: BOOK HEAVY [i.e., “the book is very heavy”]). Covert signing, that is, instructing the participants to “try to sign the sentence ‘in your head’, as if you were practicing it,” was used in preference to actual signing, to try to isolate the planning stage rather than the production requirements for the task—the production of sign involves different articulators than those for speech, and these were not the focus of this exploration. Broca’s area was activated by this task in BSL signers, just as it was activated by a similar covert speaking task in hearing English-speaking volunteers. Pettito et al. (2000) in a PET study of production and perception of single signs, obtained data from users of two signed languages: ASL and Langue des Signes Québécois. They, too, found that activation during production was restricted to the LH and included Broca’s area. Similar findings for the production of single signs in deaf users of ASL are reported by other groups (Emmorey et al., 2003; Kassubek, Hickok, & Erhard, 2004; San Jose-Robertson, Corina, Ackerman, Guillemin, & Braun, 2004). In a direct comparison of signed and spoken narrative production by hearing native signers, Braun, Guillemin, Hosey, and Varga (2001; see also Horwitz et al., 2003) showed that identical circuits were recruited for both types of language planning. Every neuroimaging study to date reports activation in the left inferior frontal regions for signed language production and planning. Broca’s area is always involved, and LH dominance is always observed.

Because the LH dominates for control of right-hand actions and most people are right-handed one might suspect that hand preference contributes to the strong laterality observed in signed language production. However, Corina, San Jose-Robertson, Guillemin, High, and Braun (2003) addressed this by showing that producing one-handed verbs in ASL engaged Broca’s area, whether the dominant right or nondominant left hand was used. Right-hand dominance in sign production therefore is not likely to be the immediate cause of LH superiority in signed language production.

The robust nature of the left-lateralized sign production system is also supported by the finding that it appears to be uninfluenced by the iconicity of the sign. Many signs appear to bear some relationship to their

real-world referents. For example, a sign may trace the outline of a referent (e.g., the BSL sign HOUSE, which traces the outline of a house) or may refer to a particular visual characteristic of the referent (e.g., the BSL sign CAT, which traces a cat's whiskers, but means "cat"). Despite this, sign-aphasic patients are often unable to produce iconic signs in response to prompts such as "show me the sign for 'toothbrush,'" but can produce the same actions elicited as pantomimed gesture—"how do you brush your teeth?" (see Corina et al., 1992; Marshall et al., 2004). That is, they show a dissociation between signed language (impaired) and gesture (unimpaired). Imaging studies, too, suggest that iconicity fails to influence the cortical regions activated in the production of signed language (see Emmorey et al. [2004] and San Jose-Robertson et al. [2004] for further discussion of the role of iconicity in signed language production).

Production in Perception/Perception in Production?

The impression from the review so far may be that production (especially of syntactic forms) makes exclusive use of Broca's area, whereas sign perception only activates Wernicke's area. But whether perception or production is tested, both Wernicke's and Broca's areas are active (see Figure 2a for activation of frontal regions during perception). Although frontal regions are certainly implicated in planning signed language production, they are also involved in passive perception of sign. Superior temporal regions, although very active in perceiving signed language, are also active in planning and production. This is also true for spoken language (Blumstein, 1994). Some recent discoveries suggest there are circumscribed and specialized regions of the frontal lobe that, in addition to playing a role in production, are also sensitive to perceiving specific actions. These might have evolved to help us imitate actions produced by our fellow humans. To the extent that we perceive language being "made" by other humans, they may be implicated in producing and perceiving language (mirror-neuron theory; Rizzolatti & Craighero, 2004). Whether or not mirror-neuron theory is accepted as a basis for understanding how perception is translated into action, it

seems that we cannot perceive language (spoken or signed) without, at the same time, invoking brain systems that are involved in its production. Similarly, in producing a language utterance, mechanisms are activated that are used in perception. When it comes to language, perception and production are entwined. This was hardly suspected from the lesion studies, where perception and production difficulties are clearly differentiated. However, some neurolinguistic theories, such as the motor theory of speech perception (Lieberman & Mattingley, 1985), anticipated such a link and are now enjoying renewed interest in the light of mirror-neuron theory. Motor-theoretic ideas were concerned with speech, and spoken language does not make essential use of spatially articulated gestures of the hands and arms. One possible implication for sign processing is that connections between brain regions important for selection-for-production and representation of the different articulators (hands, arms, head, and face) and their positions in relation to the body in space may be especially implicated when sign (but not speech) is being processed. Where in the brain are these connections to be found? They are those that link inferior frontal and superior parietal regions (see Corina & Knapp, 2006). As we will see (below), there are more indications that signed language may make special use of the parietal function of body-in-space representation.

When Sign Is Special

We have claimed that when it comes to language, whether signed or spoken, the left perisylvian regions are critical. That is, left invariance, right variability can be shown to apply as much to signed language processing as to spoken language processing—as long as the conditions of sign and speech are structured appropriately. It should be impossible to infer whether the images in Figure 2a reflect sign processing in a native signer or speech processing in a hearing native English speaker (as long as we "mask out" the primary sensory regions for vision and for audition and other regions that may be specialized input regions for visual analysis of gesture and for auditory analysis of complex sound). When the data tell the scientist "there are no differences" the first thing she thinks is "perhaps

I have not tested the hypothesis sufficiently carefully.” Detailed studies of particular signed language constructions are underway, but so far the results are confusing. For example, use of classifiers in signed languages might be predicted to be especially reliant on spatial analysis and therefore involve the RH. Although Emmorey et al. (2002) reported RH and LH involvement in producing ASL classifiers, a BSL comprehension study found greater LH activation for sentences with many classifier signs (topographical sentences) in contrast to sentences with fewer classifiers (MacSweeney et al., 2002a). Where both studies agreed was that inferior and superior parts of the parietal lobe were especially implicated (left and right parietal regions in the Emmorey et al. study; left in MacSweeney et al.). These parietal regions are not generally involved in spoken language processing but are implicated in all sorts of nonlinguistic tasks that require spatial analysis of a scene as well as tasks that reflect awareness of parts-of-body positions. The laterality difference between these studies may have been due to the different task requirements: production in response to picture stimuli in the Emmorey et al. study and comprehension of signed sentences in the MacSweeney et al. study. It is possible that greater mapping demands (picture to sign) in the Emmorey et al. studies led to increased demands on the right parietal lobe.

Another way in which sign might be special is in its use of nonmanual markers, especially the uses of the face. Nonmanual features can function linguistically in many signed languages (e.g., McCullough, Emmorey, & Soreno, 2005, for ASL). For hearing people who do not sign, facial expression and facial intention processing is right-lateralized. How does the signer’s brain deal with such nonmanual markers? Perhaps it can separate face actions out so that linguistic ones get processed along with manual signs in the LH, whereas emotional ones are right sided, following the right-sided pattern in hearing nonsigners. This idea was tested on six BSL signers with unilateral brain damage (Atkinson, Campbell, Marshall, Thacker, & Woll, 2004). The linguistic function of negation was investigated. Negation (that something is *not* the case) is considered to be a syntactic property because specific sentence structures may be used to express the

negation of an event (I hit the ball/ I *did not* hit the ball). We have already noted that syntactic processing in signed languages appears to engage the same left perisylvian regions as syntactic processing in spoken languages. In BSL, headshake, a furrowed brow, and a frowning facial gesture are the nonmanual actions constituting the default (or unmarked) way of expressing negation. Because negation is considered syntactic, the investigators predicted that processing nonmanual negation ought to be difficult for patients with LH lesions, who had language impairments. Contrary to prediction, however, all three patients with left-sided lesions, who were aphasic for signed language, understood negation perfectly when it was expressed nonmanually. Negation can also be expressed in BSL by a manual negation marker such as the sign, [NOT]. The aphasic patients failed to understand the sign, [NOT], just as they failed to comprehend other manual signs. However, patients with right-sided lesions, who were not aphasic, had no difficulty with the manual sign, [NOT], but failed to understand nonmanual (facial) negation. This unexpected finding alerts us to the possibility that negation might not always be accomplished syntactically, but by other (pragmatic and prosodic) means. These pragmatic processes may be processed by the RH rather than the LH (see above). Functionally, the head and face actions might be construed as a comment on the statement rather than being integral to it. Perhaps nonmanual negation in BSL might be glossed as: “The dog has a bone. I don’t think so!” Thus, just because our theory of language might predict that negation should be a feature of syntax, this does not mean that this is how it is always processed in a signed language. Indeed, this lesion study raises an important point in considering the design and interpretation of studies of signed language and the brain. The prediction that negation would be left-lateralized for signed languages was based on two assumptions: (a) grammatical negation is a function of syntax and (b) syntactic processing is left-lateralized in the brain. The first assumption, however, was very much based on theories of how negation is processed in spoken languages. We should be open, however, to the possibility that signed languages may be structured in ways both similar and different to spoken languages. In this case, the results suggest that the

default form of negation in BSL might be better understood as part of prosody/pragmatics rather than a process operating at the syntactic level. However, this interpretation depends on the second assumption, which, again, is motivated by what we know of the neural bases supporting the syntactic processing of speech. This example highlights how we should be cautious when interpreting studies of the neurobiological bases of linguistic processing—both in terms of implications for (and from) linguistic theory and our understanding of brain function.

Deaf and Hearing Native Signers—Differences in Brain Activation

On the whole, we have suggested that the patterns of brain localization for deaf native signers processing signed language look very similar to those for spoken language processing in hearing native speakers. However, does hearing status impact upon the neural systems recruited for language processing by native signers? A number of studies have explored this question by contrasting hearing children of deaf signers, with deaf children of deaf signers in terms of brain activation (see MacSweeney et al., 2002b, 2004, 2006; also Neville et al., 1997). Some differences between these groups can be found. In particular, auditory processing regions in the temporal lobe (see Figure 1) are less active for signed language (and sign-like nonsense gestures) in hearing than in deaf native signers. It is likely that auditory processing tends to dominate in these cortical regions, even when a visual language is learned first. In deaf people who do not receive auditory input, these regions can be recruited to process input from other modalities. The possibility that some brain regions normally “led by” one sensory process might be used for others when circumstances and experience dictate is discussed elsewhere (cross-modal plasticity: see Campbell & MacSweeney, 2004; also Bavelier & Neville, 2002).

Nonlinguistic processing can also be tested in hearing signers. Being deaf from birth and being exposed to a sign early in life can have dissociable effects on brain function (see Bavelier & Neville [2002] and Bavelier et al. [2006] for reviews). Bosworth and Dobkins (2002) found that the processing of simple

displays of dot movement was more efficient in the LH than the RH in people who had early exposure to signed language, regardless of whether they were deaf or hearing. Both groups of signers differed from hearing nonsigners in this respect. In an fMRI study, Bavelier, Brozinsky, Tomann, Mitchell, and Liu (2001), reported that visual attention to the periphery was more efficient in deaf than in hearing people—even though both groups were signers. Here, the importance of attending to peripheral visual events, which is a functional consequence of hearing loss, drives the deaf brain to reconfigure.

A different sort of functional plasticity can be seen in relation to auditory processing regions. Fine, Finney, Boynton, and Dobkins (2005), using fMRI, found that in deaf, but not hearing signers, the movement of visible dot patterns caused activation in regions that support hearing (and only hearing) in hearing people, that is, in auditory cortex in the superior temporal lobe. This suggests that “unused” auditory cortex can be colonized by vision. Greater activation in this region has also been reported in deaf compared with hearing signers when watching BSL and nonsense gesture (MacSweeney et al., 2004).

Thus, both signed language exposure and congenital deafness may reset the tracks of brain development to diverge from those with which we may be familiar from studies of hearing people and spoken language acquisition. Different patterns of brain function may emerge that are more efficient for the specific environment or circumstances of the individual.

Brain Plasticity—Lifetime Events Can Affect the Brain

Earlier in this review we cautioned the reader that patterns of localization for language processing are not immutable and that a range of environmental and cultural factors can affect the course of development of specialization of particular brain circuits. These are confined not only to events that occur early in life (such as prelingual deafness) but also to events that occur later (like the writing system to which a child, aged 7 or 8 years, may be exposed). Events in adulthood may also be important. To date, very little is known about the cortical systems involved

when an individual becomes deaf later in life or when a signed language is learned late or as a second language. The finding of Newman et al. (2002) with hearing late learners of ASL is unlikely to transfer directly to deaf late learners of a signed language. Hearing late signers have a well-established first (spoken) language. By contrast, deaf late learners of a signed language, who constitute the majority of deaf signers and whose language development tends to lag that of the early signer (Mayberry & Lock, 2003), do not have a secure first language, learned in infancy. In these people, the left inferior frontal gyrus may play a greater role in language processing than it does in deaf native signers (MacSweeney, Waters, Brammer, Woll & Goswami, submitted). This region has been implicated in the less well-learned language in speech bilinguals (Klein et al., 2006). Its role in relation to signed language learning has yet to be fully elaborated.

The impact of age of onset of deafness and age of signed language acquisition are both important questions, which are now being addressed. Such studies will allow us to address fundamental questions about how experience shapes brain development. Many other questions also currently remain unanswered regarding the impact of the often-complex language background of deaf people on brain function. For example, how might the deaf person's literacy affect the functional organization of their brain for other language skills? Could we even be presented with a unique pattern relevant only to one specific signed language, in one particular signer, whose language background may be utterly idiosyncratic?

Conclusion

This short tour of recent developments in the cortical imaging of signed language processing has to a large extent confirmed the findings of the now classical lesion studies of Poizner and colleagues, 20 years ago. Signed language, like spoken language, makes special use of the left perisylvian regions of the brain. Where differences can be shown between sign and speech they can, on the whole, be ascribed to the different input modalities of the language system—auditory for spoken language, visuospatial for signed language. The specialization of cortical networks for language pro-

cessing does not appear to be driven either by the acoustic requirements for hearing a spoken language or by the articulatory requirements for speaking. It seems likely, therefore, that it is the specialized requirements of language processing itself, including, for instance, compositionality, syntax, and the requirements of mapping coherent concepts onto a communicable form, that determine the final form of the specialized language circuits in the brain. Even the disagreements in the literature, especially those concerning the relative importance of the RH in processing sign, do not trouble this basic insight. It is probably more constructive to pose a somewhat different question: How might signed language use specific brain specializations that are unlikely to be involved in spoken language processing? Even within the 10 or so years of observing the healthy human brain processing signed language, we have moved from general to more specific, refined hypotheses with respect to this question.

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