73 The Neurobiology of Sign Language Processing

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ABSTRACT By investigating sign languages, which are purely visual and not derived from auditory-vocal processes, we gain unique insight into the neurobiology of language. Sign languages represent a powerful tool with which to test constraints and plasticity of the language system. In this chapter we review the current literature on the neural systems supporting the production and comprehension of signed languages, focusing on native users. The literature clearly shows that the left-lateralized perisylvian language network identified as reliably engaged during spoken language processing, involving the core regions of the inferior frontal gyrus and superior temporal cortex, is recruited during sign language processing. Similarity of processing has also been identified in aspects of the timing of the linguistic processing of sign and speech. However, there are important differences in how the brain processes sign and speech. The left parietal lobe appears to play a particularly important role in sign language production and comprehension. In particular, parietal cortex is involved in processing the linguistic use of space, in phonological encoding (left supramarginal gyrus), and in self-monitoring during sign production (left superior parietal lobule).

Sign languages arise wherever Deaf communities come together, and they differ across countries. For example, American Sign Language (ASL) and British Sign Language (BSL) are mutually unintelligible. Importantly, the grammar of signed languages is not dependent on the surrounding spoken language. Further, studies have clearly shown that deaf (and hearing) children who learn a signed language from birth show the same developmental milestones in their language acquisition as hearing children learning a spoken language (Meier & Newport, 1990). Therefore, we can compare the neural systems established to support language production and comprehension in those who have acquired a signed or a spoken language as their first language.

In this chapter we review the literature to date and show that signed and spoken language processing both recruit modality independent neural circuits (e.g., the perisylvian cortices, including the inferior frontal and superior temporal gyri) and modality-dependent neural regions (e.g., left parietal cortex for sign language processing). Evidence from electroencephalography (EEG) and magnetoencephalography (MEG) indicates that the temporal neural dynamics of language production and comprehension is similar for signed and spoken languages, despite sensorimotor differences. Finally, we explore the role of parietal cortex in supporting spatial-processing demands that are unique to sign languages.

The Neurobiology of Sign Language Production

The primary linguistic articulators for sign language are the hands and arms, which are independent, symmetrical articulators; in contrast, the speech articulators include the larynx, velum, tongue, jaw, and lips, which are all located along the midline of the body. Although much is known about the neural networks involved in speech-motor control, we know very little about the neural systems that control manual sign production. Nonetheless, linguistic and psycholinguistic research has revealed both modality-independent and modality-specific properties of sign and speech production (see Corina, Gutierrez, & Grosvald, 2014 for a review). For example, both sign and speech production require the phonological assembly of sublexical units (handshape, location, and movement for sign language), as evidenced by systematic production errors (slips of the hand; e.g., Hohenberger, Happ, & Leuninger, 2002). Both signed and spoken languages encode syllables and constrain syllable internal structure in a similar manner (e.g., Berent, Dupuis, & Brentari, 2013). Both sign and speech production involve a two-stage process in which lexical semantic representations are retrieved independently of phonological representations, as evidenced by tip-of-the-tongue and tip-of-the-finger states (Thompson, Emmorey, & Gollan, 2005). Syntactic priming in sentence production occurs for both signed and spoken languages (Hall, Ferreira, & Mayberry, 2015). However, language output monitoring likely differs for sign and speech due to differences in perceptual feedback: speakers hear themselves speak, but signers do not see themselves sign (Emmorey, Bosworth, & Kraljic, 2009). Below, we explore the evidence for shared functional neural substrates for sign and

speech production, as well as evidence for neural substrates that are specific to sign production.

Modality-independent cortical regions involved in language production Both sign and speech production are strongly lateralized to the left hemisphere. Signers with left, but not right, hemisphere damage produce phonological and semantic paraphasias (Hickok, Bellugi, & Klima, 1996). Phonological paraphasias in sign language involve the substitution of one phonological unit for another, as illustrated in figure 73.1. Recently, Gutierrez and colleagues used functional transcranial Doppler sonography (fTCD) to investigate hemispheric lateralization during natural (nonrestricted) speech and
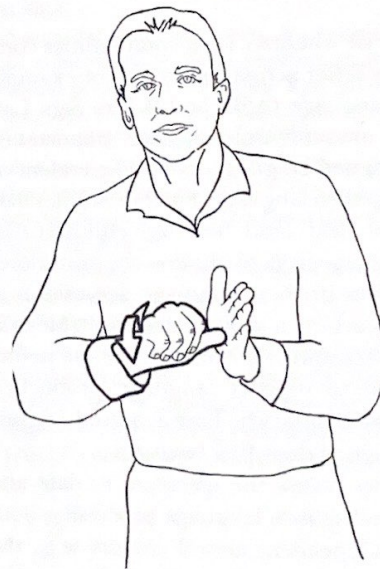

Error

Movement error
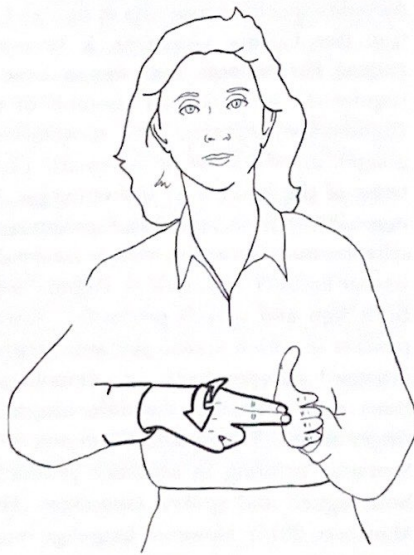
Screwdriver

Handshape error

FIGURE 73.1 Examples of phonological paraphasias in ASL created by movement or hand-shape substitutions.

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sign production in neurotypical adults (Gutierrez-Sigut et al., 2015; Gutierrez-Sigut, Payne, & MacSweeney, 2016). fTCD is a noninvasive technique that measures changes in blood flow velocity within the middle cerebral arteries. Hearing participants who were bilingual in English and British Sign Language (BSL) exhibited stronger left lateralization for sign than speech production when performing verbal fluency tasks (Gutierrez-Sigut et al., 2015). A control experiment with sign-naïve participants indicated that the difference in laterality was not driven by greater motoric demands for manual articulation. Native deaf signers also exhibited stronger left lateralization for both covert and overt sign production in comparison to hearing bilinguals producing speech (Gutierrez-Sigut, Payne, & MacSweeney, 2016). The authors speculate that the increased left lateralization for signing may be due to modality-specific properties of sign production, such as the increased use of proprioceptive self-monitoring mechanisms or the nature of phonological encoding of signs (see below).

Within the left hemisphere, the inferior frontal gyrus (IFG) has been implicated as a key region involved in both sign and speech production. In a positron emission tomography (PET) study, Braun, Guillemin, Hosey, and Vargus (2001) asked hearing ASL-English bilinguals to produce spontaneous narratives in either speech or sign language, and a conjunction analysis that subtracted out oral and manual motor movements revealed a common activation in the left frontal operculum (BA 45, 47) for both languages. Similarly, Emmorey, Mehta, and Grabowski (2007) found that the left IFG (BA 45) was equally engaged for word and sign production when deaf signers and hearing speakers performed a picture-naming task. Horwitz et al. (2003) used probabilistic cytoarchitectonic maps of BA 45 and BA 44 along with the PET data from Braun et al. (2001) to show that BA 45 was involved in higher-level linguistic processes, while BA 44 (and not BA 45) was engaged in the generation of complex oral and manual movements. Consistent with this finding, cortical stimulation of BA 44 during picture naming and sign/pseudosign repetition by a deaf signer resulted in motor execution errors (e.g., lax or imprecise articulation), rather than phonological errors (e.g., handshape substitution; Corina et al., 1999).

Evidence that the left IFG (BA 45, 47) is involved in lexical-semantic processes during sign production comes from PET studies in which signers generated verbs in response to videos of noun signs (Corina et al., 2003; Petitto et al., 2000) or videos of transitive actions (San José-Robertson, Corina, Ackerman, Guillemin, & Braun, 2004). Greater activation was observed in the left IFG for verb generation compared to the passive viewing of nouns or of action videos, regardless of whether the

verbs were articulated with the right or left hand (Corina et al., 2003). Thus, engagement of the left IFG during verb generation is not driven by motoric factors related to the use of the dominant right hand in signing. Studies of verb generation in spoken languages have indicated that the left IFG is involved in lexical selection or the strategic control of semantic processing (e.g., Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997).

With respect to higher-level processes involved in language production, a recent MEG study by Blanco-Elorrieta, Kastner, Emmorey, and Pylkännen (2018) investigated whether the same neurobiology underlies the online construction of complex linguistic structures in sign and speech. Two-word compositional phrases and two-word noncompositional "lists" were elicited from signers and speakers using identical pictures. In one condition, participants combined an adjective and a noun to describe the color of the object in the picture (e.g., *white lamp*) and in the control condition, participants named the color of the picture background and then the object (e.g., *white, lamp*). For both signers and speakers, phrase building engaged left anterior temporal and ventromedial cortices, with similar timing. The left anterior temporal lobe may be involved in computing the intersection of semantic features (Poortman & Pylkännen, 2016), while the ventromedial prefrontal cortex may be more specifically involved in constructing combinatorial plans (Pylkkänen, Bemis, & Elorrieta, 2014). Overall, this work indicates that the same frontotemporal network achieves the planning of structured linguistic expressions for both signed and spoken languages.

Modality-specific cortical regions involved in sign language production The supramarginal gyrus (SMG) has been found to be significantly more engaged during sign than word production when deaf signers are compared to hearing speakers (Emmorey, Mehta, & Grabowski, 2007) and when sign and speech production are directly compared within hearing bimodal bilinguals (Braun et al., 2001; Emmorey, McCullough, Mehta, & Grabowski, 2014). The study by Emmorey, Mehta, McCullough, and Grabowski (2016) also implicated the SMG as a key region for sign production. This study elicited the following sign types: one-handed signs (articulated in "neutral" space in front of the signer), two-handed (neutral space) signs, and one-handed body-anchored signs (produced with contact on or near the body). A conjunction analysis comparing each sign type with a baseline task revealed common activation in the SMG bilaterally (greater involvement on the left) for all sign types. Importantly, Corina et al. (1999) found that stimulation to the left SMG resulted in phonological substitutions,

rather than motor execution errors. Further, bilateral SMG activation (larger on the left) has been found during the covert rehearsal of pseudosigns but not during the covert rehearsal of pseudowords (Buchsbaum et al., 2005). In addition, Cardin et al. (2016) recently found that linguistic knowledge modulated activation within the SMG in a phonological monitoring task (detecting target handshapes or locations). Specifically, the contrast between illegal nonsigns and real signs was significantly larger for deaf signers than for nonsigners (with increased SMG activation for nonsigns that violated phonological rules in both BSL and Swedish Sign Language). Together, these results suggest that the SMG is likely to be critically involved in the phonological decoding and encoding for sign language.

Emmorey and colleagues also reported that the superior parietal lobule (SPL) was significantly more active during sign than word production (Emmorey, Mehta, & Grabowski, 2007; Emmorey et al., 2014). These authors hypothesized that the SPL may be involved in self-monitoring overt sign output via proprioceptive feedback. Results from Emmorey et al. (2016) provide some support for this hypothesis: the production of body-anchored signs resulted in greater activation in the SPL compared to signs produced in neutral space. Greater engagement of the SPL may reflect the motor control and somatosensory monitoring required to direct the hand toward a specific location on the face or body. It is important to note that signing is not visually guided—signers do not look at their hands when they sign, and visual feedback does not appear to be used to fine-tune sign articulation (Emmorey, Bosworth, & Kraljic, 2009). Thus, the self-monitoring of sign articulation is likely to rely heavily on proprioceptive feedback. The SPL is known to play a role in updating postural representations of the arm and hand when movements are not visually guided (e.g., Parkinson, Condon, & Jackson, 2010). A recent transcranial magnetic stimulation (TMS) study by Vinson et al. (2019) has also implicated the SPL in sign production. While signers named pictures, TMS was administered to the left SPL or a control site. TMS to the SPL had a very specific effect: an increased rate of phonological substitution errors for two-handed signs that required hand contact. However, TMS did not slow or otherwise impair performance. Thus, TMS decreased the likelihood of detecting or correcting phonological errors during otherwise successful bimanual coordination. Interestingly, overt articulation is not required to engage the SPL for sign language production. MacSweeney et al. (2008) reported greater left SPL activation, extending into the superior portion of the SMG, when deaf signers made phonological judgments about the sign names of pictures (Were they produced at the same location?) than in hearing speakers making a phonological decision about words (Do they rhyme?). Although these regions appear to be more involved for signed than spoken language processing, a conjunction analysis by MacSweeney et al. (2008) showed that form-based judgments about both languages recruited the left SPL (extending into SMG) to a significant degree. This result suggests that regions within parietal cortex may also be involved in phonological processes that are supramodal. The inferior parietal lobule has been implicated in phonological processing during reading and as a component of phonological working memory for speech. Supramodal processes that might be subserved by parietal cortex include sublexical sequencing or assembly processes that are independent of the modality of the to-be-combined phonological units. However, further research is needed to establish the nature and location of shared language-production processes within parietal cortex.

The Neurobiology of Sign Language Comprehension

Although we most often see people when we speak to them—that is, we perceive audiovisual speech—audition is key to speech perception. In contrast, signed languages must be perceived through the visual modality alone. Despite these differences in the modality of perceiving signed and spoken languages, the shared goal is comprehension. As with production, numerous psycholinguistic studies have shown extensive similarities between sign and speech comprehension processes. For example, studies have found evidence for categorical perception (Palmer, Fais, Golinkoff, & Werker, 2012), phonological and semantic priming (Meade, Lee, Midgley, Holcomb, & Emmorey, 2018), Stroop effects (Dupuis & Berent, 2015), incremental processing (Lieberman, Borovsky, & Mayberry, 2018), and many other parallels between the processes involved in comprehending signed and spoken languages (see Emmorey, 2002 for review). Below we explore the evidence for shared functional neural substrates for sign and speech comprehension, as well as the evidence for neural substrates that are specific to sign comprehension.

Modality-independent cortical regions involved in language comprehension As in spoken language users, damage to the left posterior superior temporal cortices and inferior parietal cortices typically leads to problems with sign language comprehension (e.g., Hickok, Love-Geffen, & Klima, 2002; Marshall, Atkinson, Woll, & Thacker,

2005). Neuroimaging studies also indicate a critical role for the left hemisphere during sign language comprehension. The first fMRI study to contrast audiovisual speech perception by hearing speakers with sign language perception in deaf signers used a conjunction analysis to identify regions common to both language modalities (MacSweeney et al., 2002). A primarily left frontotemporal network involving the superior temporal gyrus and sulcus as well as the left inferior frontal gyrus, extending into the prefrontal gyrus, was identified to be involved in processing both sign language and speech (see also Sakai, Tatsuno, Suzuki, Kimura, & Ichida, 2005). Numerous studies of sign language comprehension have also identified a primarily left lateralized frontotemporal network involved in sign language perception when contrasted with nonlinguistic hand movements (MacSweeney et al., 2004), gestures (Newman, Supalla, Fernandez, Newport, & Bavelier, 2015), or transitive actions (Corina et al., 2007). Similarities in subcortical structures supporting sign and speech processing have also been reported (Moreno, Limousin, Dehaene, & Pallier, 2018). Newman, Supalla, Hauser, Newport, and Bavelier (2010a) also demonstrated the recruitment of a predominantly left lateralized network, the components of which were modulated depending on whether the ASL sentences being viewed included inflectional morphology or word order alone to convey grammatical information. Together, these fMRI studies suggest that the classic left-lateralized perisylvian network is resilient to change in the sensory modality of language.

Event-related potential (ERP) studies further suggest that the timing of processing within this network is very similar across sign and speech comprehension. For example, a similar modulation of the N400 is observed for semantic anomalies in signed sentences as in spoken sentences (e.g., Hanel-Faulhaber et al., 2014). Although there is clear evidence for a predominantly left-lateralized network recruited for sign language comprehension, the right hemisphere also plays a supporting role—just as for spoken language processing (e.g., MacSweeney et al., 2002). Newman, Supalla, Hauser, Newport, and Bavelier (2010b) investigated the role of the right hemisphere in sign language comprehension by manipulating the narrative content of ASL sentences. They reported increased activation of the right inferior frontal gyrus and superior temporal cortex in deaf signers watching ASL sentences containing narrative devices, such as affective prosody and role shift, compared to sentences that did not contain these devices. Moreover, these regions included those recruited when hearing people perceive spoken-language sentences that include these narrative features.

Modality-specific cortical regions involved in sign language comprehension   Although the overlap between the networks supporting sign and speech processing is extensive, there are some differences. Not surprisingly, direct contrasts have highlighted differences reflecting early sensory processing. Signed languages elicit greater activation than audiovisual speech in biological motion-processing regions of the posterior middle temporal gyri, bilaterally. In contrast, audiovisual speech perception in hearing participants elicits greater activation than sign language perception in deaf participants in auditory-processing regions in the superior temporal cortices (Emmorey et al., 2014; MacSweeney et al., 2002).

It is important to note, however, that although these studies show greater activation in the auditory cortices of hearing people perceiving speech than in deaf people perceiving sign language, these regions *do* respond to visual input in deaf people. This issue of crossmodal plasticity of the auditory cortices in deaf people and the extent to which these regions are involved in sign language comprehension have been topics of much recent research interest. There is mixed evidence regarding whether sign language, or any other visual stimuli, activates the primary auditory cortices in those born deaf (see Cardin et al., 2016; Scott, Karns, Dow, Stevens, & Neville, 2014). However, there are now numerous reports of increased activation in secondary auditory and auditory association cortices in superior temporal cortex (STC) in deaf compared to hearing individuals during sign language perception. This is even the case when deaf native signers are compared to hearing native signers, and sign language experience is therefore similar across groups (Capek et al., 2010; MacSweeney et al., 2004; Twomey et al., 2017).

Sign Language Makes Special Use of Space

As outlined above, the left parietal lobe appears to be particularly involved in sign language production, especially during phonological processing and self-monitoring. In addition, the left parietal lobe appears to be recruited by sign languages when spatial-processing demands are increased.

The use of space for linguistic purposes (e.g., coreference, spatial language) is unique to sign languages. In particular, signers use *classifier constructions* to express spatial relationships, in contrast to speakers, who typically use spatial prepositions or locative affixes. The handshape within a classifier construction is a morpheme that encodes information about the referent object (e.g., its semantic category or size and shape)

while the placement and movement of the hands in signing space depict the location and movement of the referent objects. Lesion studies indicate that right hemisphere damage can cause difficulties in both producing and comprehending classifier constructions, but it does not result in sign language aphasia (Atkinson, Marshall, Woll, & Thacker, 2005; Hickok, Pickell, Klima, & Bellugi, 2009). Using a picture-description task and PET imaging, Emmorey, McCullough, Mehta, Ponto, and Grabowski (2013) found that the production of lexical signs and classifier handshape morphemes engaged left inferior frontal and temporal cortices, while the expression of gradient locations and movements engaged the bilateral SPL (extending into the SMG). Emmorey et al. (2013) argued that to express spatial information, signers must transform visual-spatial representations into a body-centered reference frame and reach toward target locations in signing space.

With regard to comprehension, Capek et al. (2009) highlighted the special role of spatial processing in sign language syntax. Using ERPs, they found that syntactic violations in ASL elicited early frontal negativities that varied as a function of how space was used to create the violation. MacSweeney et al. (2004) reported greater activation in the left SMG and SPL when deaf signers viewed BSL sentences that involved classifier constructions than when they viewed sentences that did not (see also Jednorog et al., 2015). McCullough, Saygin, Korpics, and Emmorey (2012) explored this finding further and demonstrated that the left SPL and SMG were particularly engaged during comprehension sentences containing classifier constructions that expressed spatial relations between referents, rather than movement of the referent. Emmorey et al. (2013) also found that the left intraparietal sulcus was more engaged when classifier constructions expressed object location rather than object movement. Sign language processing requires attention to the location and configuration of the hands in space and is likely to explain the enhanced involvement of these regions. The semantic focus on these features when producing and comprehending classifier constructions is likely to increase these processing demands further.

Conclusion

Despite great differences in their surface forms, both signed and spoken language-processing in native users engage very similar, predominantly left-lateralized, networks. This is an important conclusion that should be taken into account in theories of hemispheric specialization for language processing. Some have argued that the left hemisphere shows a predisposition to process certain temporal aspects of auditory information that are critical to speech processing (see McGettigan & Scott, 2012 for discussion). The inference is then made, explicitly or implicitly, that this is the cause of left-hemisphere lateralization for language processing. That signed languages are also predominantly processed in the left hemisphere poses a problem for any purely auditory-based account of language lateralization. It is possible that sign languages recruit the neural infrastructure already established for spoken languages. This proposal is in line with the neuronal recycling hypothesis proposed by Dehaene and Cohen (2007) to account for the preference of the ventral occipitotemporal cortex to process written words. However, we suggest that a recycling hypothesis is unlikely to account for the left lateralization of sign languages. If the left perisylvian cortices are "specialized" for speech, then the use of these regions for sign language processing should come at a cost. That is, native learners of sign languages should show delays/deficits compared to native learners of a spoken language, but this is not the case (Meier & Newport, 1990). Although the research to date with signed languages does not allow us to answer *why* language is predominantly left lateralized in most people, it should prompt the field to generate hypotheses that are modality-independent and can account for the left-hemisphere lateralization of both sign language and speech.

Observing such striking similarities in the neural systems recruited for sign and speech processing has led the field to assume that the same processes are being carried out in these regions for both language types, using similar representations (e.g., MacSweeney et al., 2008). However, this is an assumption based on null findings of no significant differences in activation between languages. Multivoxel pattern analysis (MVPA) has been used in a number of domains to examine *patterns* of activation rather than the overall level of activation. This approach has the potential to identify common neural representations for different modes, inputs, or states. These approaches will also allow us to directly test hypotheses about the similarity of processing and the similarity of representations. Pursuing questions about the computations that occur and the representations used in the regions identified as showing overlap between sign and speech processing is likely to produce novel insights into the neurobiology of language. So, too, is pursuing the small but interesting differences that have to date been identified in the neural systems supporting sign and speech processing. The left inferior and superior parietal lobules, especially, appear to be more involved in sign comprehension, production, memory, and metalinguistic processes compared to spoken language. In sum, the study of

sign languages will continue to offer unique insights into the neuroplasticity of the language networks and representations in the brain.

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