Language in Our Hands: Neural Underpinnings of Sign Language and Co-Speech Gesture

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ABSTRACT The human ability to communicate information is not exclusive to speech-meaning can also be conveyed by the hands in sign languages and in co-speech gestures. Traditionally, the two have been studied separately, partially because each has very different properties (e.g., co-speech gesture is integrated with the speech channel; sign language is an independent, hierarchical system). This chapter brings together for the first time findings on the neural underpinnings of signs and co-speech gestures. Sign language and co-speech gestures both recruit the left hemisphere for production and involve the right hemisphere for representation of spatial events. Sign, co-speech gesture, and speech also implicate similar neural substrates for comprehension: left inferior frontal cortex, posterior superior temporal cortex, and bilateral middle temporal gyri, as well as similar electrophysiological responses to semantic violations (N400) and syntactic violations (P600). This review underscores the fact that the brain's general infrastructure for language and communication treats meaningful information coming from all channels and formats in highly similar ways.

Meaning can be conveyed by the hands in a variety of ways: through signing (used by deaf communities), pantomimed actions and emblematic gestures (often used in the absence of speech), or through gestures produced while speaking (i.e., gesticulation). This chapter focuses primarily on the first and the last phenomena, which form the endpoints of the gesture continuum (McNeill, 1992). As one moves from gesticulation toward sign language, idiosyncratic gestures used with speech are replaced by conventionalized/pantomimic gestures, linguistic properties increase, and the obligatory use of speech declines. Unlike co-speech gesture, sign languages are complete linguistic systems, exhibiting structural and language-specific constraints at the phonological, lexical, syntactic, and discourse levels.

Traditionally, the world's languages have been grouped into two classes, signed and spoken languages, based on the modality through which communicative messages are transmitted: visual-manual versus auditory-vocal. However, in the last decade it has become clear that this simple modality distinction does not

capture the fundamental multimodal complexity of the human language faculty. Spoken languages also exploit the visual-gestural modality for expression and use gestures accompanying speech, with the hands, face, and body as articulators. For example, speakers can move the fingers of an inverted V-hand in a wiggling manner while saying "he walked across" or use bodily demonstrations of reported actions as they tell narratives. Gestures contribute semantic, syntactic, and pragmatic information to the verbal part of an utterance. To be able to understand the neural infrastructure of our language faculty as a whole, we need to take into account the composite multimodal utterances of spoken languages—that is, both speech and co-speech gestures. Similarly, mapping the neural architecture for manual gestures that form a hierarchical linguistic system in sign languages is also necessary for a general account of the neural bases of the human language faculty.

Because language on the hands has very different properties for sign languages and for co-speech gesture, we discuss their neural underpinnings in separate sections. When appropriate, we highlight relevant parallels and differences in each section and situate their neural processing in the context of what we know for spoken language.

The neurobiology of sign language

Sign languages exploit visual-spatial contrasts at the phonological level (e.g., locations on the body constitute contrastive units of form), at the morphological level (e.g., temporal aspect is marked by distinct patterns of movement), at the syntactic level (e.g., grammatical roles are distinguished through the use of locations in signing space), and at the discourse level (e.g., topics can be associated with spatial locations). Despite this dependence on visual-spatial processing, the left, rather than the right, hemisphere is critical for producing and comprehending sign language. Damage

to the left hemisphere produces sign language aphasias that are parallel to spoken language aphasias, while damage to the right hemisphere does not. Signers with damage to left frontal cortex often exhibit nonfluent aphasia, characterized by effortful signing with reduced grammatical morphology. Lesions to more posterior regions within the left hemisphere produce fluent aphasias, characterized by fluent signing with persistent paraphasias (phonological or semantic errors). Signers with left temporal lobe damage also have much poorer sign comprehension compared to those who suffer damage to the right hemisphere or to other left-hemisphere regions.

In this chapter, we focus on a few key left-hemisphere brain circuits that have been identified as supporting language functions, and consider whether they are specific to spoken language and whether adaptations within these neural circuits are observed for sign language. Although there is clear overlap between the neural substrate for both language comprehension and production, these functions are discussed separately in order to explore the particular effects of distinct motor systems on language production and different perceptual systems on language comprehension.

SIGN LANGUAGE PRODUCTION The left inferior frontal gyrus (IFG), including Broca's area (BA 44 and 45), has long been known to be involved in speech production. Several types of data indicate that this region is equally important for sign production. Using positron emission tomography combined with probabilistic cytoarchitectonic mapping, Horwitz et al. (2004) examined the roles of BA 44 and 45 in the production of spoken and signed narratives by hearing bilinguals who were native users of American Sign Language (ASL) and English. Horwitz et al. (2004) found involvement of BA 45, but little or no involvement of BA 44, during language production (either signing or speaking) compared to a baseline condition in which participants produced complex nonlinguistic oral or manual articulations. Similarly, extensive activation in BA 44, but not in BA 45, was observed for the nonlinguistic oral or manual control tasks compared to rest. This pattern of results suggests that BA 44, rather than BA 45, is engaged during the production of complex movements of the oral or manual articulators and that BA 45 is more likely engaged in articulator-independent aspects of language production.

Consistent with this hypothesis, Emmorey, Mehta, and Grabowski (2007) found that left IFG (primarily BA 45) was equally engaged when deaf signers and hearing speakers overtly named pictures (contrasted with a standard baseline task that required overt motor responses

without lexical access). Further, Corina, San Jose-Robertson, Guillemin, High, and Brown (2003) reported activation in left inferior frontal cortex (primarily BA 45, extending into BA 47) when deaf right-handed signers generated verb signs with either their right or left hand, compared to repeating one-handed noun signs. These results suggest that more anterior regions of left inferior frontal cortex (BA 45 and 47) are engaged in modality-independent lexical search and retrieval processes and that this functional specialization is unaffected by the left-handed production of signs.

One striking difference between signed and spoken language production is the involvement of the left superior parietal lobule (SPL) during signing but not speaking (e.g., Emmorey et al., 2007). The precise role of left SPL in sign production is unclear, but this region is known to be involved in the online control and programming of reach movements to target locations, and for sign production, the hand must move to specific locations on the torso, face, or nondominant hand. In addition, SPL plays an important role in the assessment and monitoring of self-generated hand and arm movements. Because signing is not visually guided (i.e., signers do not look at their hands), sign language production must involve somatosensory monitoring of hand and arm movements and of hand postures and configurations.

Finally, the neural systems that support the production of pantomimed gestures and signs are nonidentical, even when signs are indistinguishable from pantomimes (e.g., the signs BRUSH-HAIR and HAMMER resemble the actions of hairbrushing and hammering). Emmorey, McCullough, et al. (2011) asked deaf signers to generate either pantomimed actions or iconic ASL verbs in response to pictures of manipulable objects. Verb generation engaged left IFG, as found in previous studies of both signed and spoken word generation, whereas pantomime generation engaged bilateral superior parietal cortex. These findings are consistent with data from lesion studies in which aphasic signers were reported to be impaired in sign production (e.g., making phonological and semantic errors), but their production of pantomimes was spared (Corina et al., 1992; Marshall, Atkinson, Smulovitch, Thacker, & Woll, 2004).

In sum, very similar left-hemisphere regions are engaged for signed and spoken language production. Left inferior frontal cortex is critically involved in the production of both signs and words, with the more posterior region (BA 44) engaged in phonetic and phonological encoding and more anterior regions (BA 45 and 47) engaged in lexical-semantic processes. Left

superior parietal cortex is more involved in signing than speaking, most likely because this region is functionally specialized for the control and monitoring of arm and hand movements with respect to a bodycentered framework. Finally, pantomimed actions and sign production rely on partially segregated neural systems, with sign production relying differentially on left frontotemporal cortices involved in lexical retrieval.

SIGN LANGUAGE COMPREHENSION Not surprisingly, speech comprehension engages primary and secondary auditory cortices within superior temporal cortex bilaterally, and recent research indicates that phonological processing for spoken language is associated with the posterior superior temporal sulcus (STS) bilaterally (see Hickok & Poeppel, 2007). Given that sign languages are perceived visually rather than auditorally, is there any evidence that phonological processing of signs engages superior temporal cortex? The answer is yes.

First, many neuroimaging studies report bilateral activation in posterior superior temporal cortex during sign language comprehension (see figure 56.1). Second, evidence that posterior STS is engaged in phonological processing comes from studies that examined

linguistically structured pseudosigns. Petitto et al. (2000) found that viewing both pseudosigns and real signs engaged superior temporal cortex bilaterally for deaf signers, but no activation in this region was observed for hearing individuals who had not acquired a sign-based phonological system (figure 56.1B). Emmorey, Xu, and Braun (2011) reported that pseudosigns activated left posterior STS to a greater extent for deaf ASL signers than for hearing nonsigners (figure 56.1C). Increased left STS activation for deaf signers was hypothesized to reflect heightened sensitivity to body movements that conform to the phonological structure of ASL. Left STS may be significantly more active for deaf signers than for hearing nonsigners because neurons in this region become particularly receptive to body movements that are linguistically structured and constrained.

The location and size of the neural response to signs within superior temporal cortex is modulated by hearing status and linguistic knowledge. In a functional MRI (fMRI) study investigating the comprehension of British Sign Language (BSL) sentences, MacSweeney et al. (2002) found that deaf signers exhibited greater activation in a more anterior region of left superior temporal gyrus (STG) compared to hearing signers (figure 56.1D).

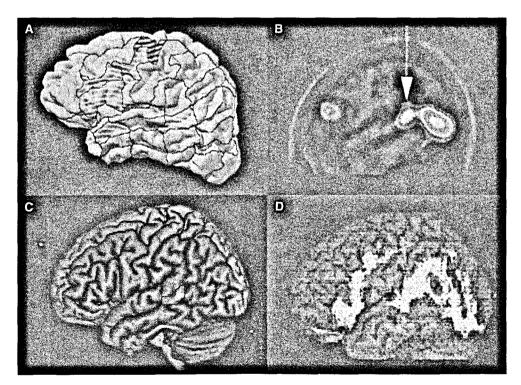


FIGURE 56.1 Illustration of left-hemisphere activations when deaf signers comprehend sign language. (A) Signed sentences vs. nonsense signs from Neville et al. (1998). (B) Signs and pseudosigns vs. fixation baseline from Petitto et al.

(2000). (C) Greater activation for deaf signers than for hearing nonsigners for pseudosigns from Emmorey, Xu, & Braun (2011). (D) Signed sentences vs. a still image of the signer from MacSweeney et al. (2002). (See color plate 49.)

These authors suggested that for hearing signers anterior left STG may be privileged for processing heard speech and therefore is not engaged during sign language processing. In the absence of auditory input, deaf signers recruit auditory regions for processing sign language, as well as other nonlinguistic visual and somatosensory stimuli (e.g., Karns, Dow, & Neville, 2012). For deaf individuals, activation extends more anteriorly along STG when comprehending sign language compared to hearing signers. This more anterior region may not be as engaged for hearing sign-speech bilinguals because this area is adjacent to primary auditory cortex, which may preferentially respond to auditory speech over visual sign language input.

In addition, a recent MEG study by Leonard et al. (2012) revealed that both signs and words activated superior temporal cortex during a relatively late time window associated with lexical-semantic processing (300–500 ms after stimulus onset), but only speech for hearing individuals activated these regions during early sensory processing (80-120 ms). Leonard et al. (2012) concluded that activation in superior temporal cortex is associated with lexical processing of signs and does not result from a rewiring of visual sensory input to auditory cortices due to congenital deafness. Further, Cardin et al. (2013) found that when viewing signs, increased activation in left STS was driven by linguistic knowledge rather than by auditory deprivation. Deaf individuals who were not signers ("oral deaf") did not show increased activation in left STS compared to hearing nonsigners when viewing signed input. Thus, left-hemisphere STG/STS activation when comprehending sign language appears to arise from linguistic processing rather than from early (low-level) visual processing.

Several event-related potential (ERP) studies have found that semantic violations in sign language elicit an N400 response that is parallel to what has been reported for spoken and written language. The N400 is hypothesized to index semantic processing and integration. In addition, Capek et al. (2009) reported that syntactic violations in ASL that involved reversed verb agreement elicited a left anterior negativity (LAN) followed by a later, more broadly distributed P600 response. For spoken language processing, the LAN component is hypothesized to index early automatic syntactic processes, while the P600 is hypothesized to reflect syntactic reanalysis and error correction. These results indicate that syntactic and semantic processes are supported by distinct brain systems for both signed and spoken languages.

Finally, the comprehension of pantomimed gestures can be preserved in the face of sign language

comprehension deficits (Corina et al., 1992; Marshall et al., 2004), suggesting that neural systems that support symbolic gesture and sign language processing are nonidentical. However, there are no reports indicating a double dissociation in which pantomime comprehension is impaired but sign language comprehension is spared. Thus, it is likely that at some level of processing. pantomimed gestures and sign language share a common neural substrate. Emmorey, Xu, Gannon, Goldin-Meadow, and Braun (2010) found very similar patterns of activation within bilateral posterior temporal cortex when deaf signers passively viewed pantomimed actions and ASL signs, but with evidence for greater activation in left IFG when viewing ASL signs. Xu, Gannon, Emmorey, Smith, and Braun (2009) found that comprehending symbolic gestures (pantomimes and social emblems, such as the "be quiet" gesture) and their spoken language equivalents both engaged left IFG and left posterior middle temporal gyrus (MTG). The authors suggested that these areas are part of a domain-general semantic network for human communication. Recently, Rong, Xu, Emmorey, Braun, and Hickok (2012) reanalyzed the Xu et al. (2009) data using a region of interest (ROI)-based multivariate pattern classification method and reported modalityspecific responses within the posterior MTG ROI. More medial and posterior voxels responded preferentially to symbolic gesture and more anterior and lateral voxels responded preferentially to speech. This suggests that there are subregions in posterior MTG that are sensitive to the modality of input.

In sum, signed and spoken languages rely on very similar neural substrates for comprehension, including left inferior frontal cortex (see figure 56.1A and 56.1D), superior temporal cortex, and bilateral middle temporal cortex. Furthermore, the same electrophysiological responses to semantic violations (N400) and syntactic violations (LAN and P600) are observed for both language types. Lastly, sign language comprehension can be impaired in the face of successful pantomime comprehension, but it appears that understanding both signs and pantomimic gestures engages left posterior MTG.

The neurobiology of co-speech gesture

Investigations of the neurobiology of co-speech gesture have focused primarily on how information conveyed by a manual gesture is integrated with information conveyed by the accompanying speech. Co-speech gestures can display semiotic complexity of different types (e.g., points, demonstrations of objects and events), have different communicative functions (e.g., emphasis,

disambiguation, speech acts), and vary in their relation to speech (e.g., conveying redundant or complementary information). Neuroimaging research has focused mostly on "iconic" gestures that represent objects and events by bearing partial formal resemblance to them (e.g., a chopping gesture while describing the steps of a recipe). While such gestures may resemble pantomimic actions, the meaning of co-speech gestures is often ambiguous and depends on speech for interpretation (e.g., Habets, Kita, Shao, Özyürek, and Hagoort, 2011).

Co-Speech Gesture Production Unlike sign languages, little is currently known about the neural regions engaged for gestures produced while speaking because they are difficult to study using neuroimaging techniques due to movement artifacts. Lesion studies (e.g., aphasia) often involve only a few case studies (e.g., Rose, 2006), and aphasic patients often use gestures in the absence of speech, making it difficult to infer the localization of co-speech gesture production.

Nonetheless, data from healthy participants suggests that hand preference for co-speech gestures is determined by the lateralization of language. Kimura (1973a, 1973b) found that right-handers with an (assumed) left-hemisphere language dominance produced more right-hand gestures than left-hand gestures, and viceversa. However, a study with split-brain patients (Kita & Lausberg, 2008) showed that some gestures that involve spatial imagery can be generated by the right hemisphere (specifically, iconic gestures that situate referents in gesture space, such as an inverted V-shaped hand with wiggling fingers to depict someone walking). Interestingly, such gestures resemble classifier predicates used in spatial language in sign languages, which also recruit the right hemisphere in both production and comprehension (e.g., Emmorey et al., 2013; Hickok, Pickell, Klima, & Bellugi, 2009).

Co-speech gesture comprehension: Event-related potential studies

ERP studies of co-speech gestures have mostly focused on the N400 component to investigate whether co-speech gestures evoke semantic processing. The earliest studies isolated gestures from the accompanying speech and examined how they modulated the upcoming words or how they were processed following images. Kelly, Kravitz, and Hopkins (2004) found that ERPs to spoken words (targets) were modulated when these words were preceded by gestures (primes) that contained information about the size and shape of objects that the target words referred to (e.g., tall, wide, etc.).

Compared to matching target words, mismatching words evoked an early P1/N2 effect, followed by an N400 effect, suggesting an influence of gesture on spoken words first at the level of "sensory/phonological" processing and later at the level of semantic processing. Wu and Coulson (2007) found that semantically incongruous gestures presented after cartoon images elicited a negative-going ERP effect around 450 msec, in comparison to gestures congruent with the cartoon image.

Gestures presented in a speech context produced similar results. Holle and Gunter (2007) asked subjects to listen to a sentence in which an ambiguous noun was accompanied by a gesture that disambiguated the word (e.g., "ball" with a playing ball gesture vs. a dancing gesture). An N400 effect was observed to a relevant word later in the sentence if its meaning did not match the meaning indicated by the gesture earlier in the sentence. In an ERP study, Özyürek, Willems, Kita, and Hagoort (2007) investigated the integration of cospeech gestures and spoken words to a previous sentence context. Sentences had critical words accompanied by gestures. Either the word or the gesture could be semantically anomalous or congruent with respect to the context set up by the sentence. Semantically anomalous gestures and anomalous words elicited identical N400 effects. The time course of integration of meaningful information derived from gestures did not differ from that conveyed through spoken words.

Finally, Habets et al. (2011) showed that the closer speech and gesture were temporally to each other, the more likely they were to be integrated with each other (i.e., when speech and gesture were simultaneous or when speech was delayed by 160 or 360 msec in relation to the gesture). ERPs time-locked to the speech onset showed a significant difference between semantically congruent versus incongruent gesture-speech combinations for the N400 component with SOAs of 0 and 160 msec, but not for the 360 msec SOA.

Few studies have investigated the neural infrastructure of noniconic beat gestures, which are short, rhythmic hand movements that co-occur with an emphasized segment of the speech. Holle et al. (2012) showed that such gestures facilitate the syntactic processing of speech. German-speaking participants were shown sentences with either the canonical (dominant) subject-object-verb (SOV) German word order or sentences with the less dominant object-subject-verb (OSV) word order. The sentences were presented either with or without beat gestures that co-occurred with the grammatical subject. The OSV sentences without an accompanying gesture elicited a P600 effect at the verb compared to the canonical SOV sentences. However,

the P600 effect disappeared when the beat gesture emphasized the grammatical subject in the OSV sentences. Beat gestures made the grammatical roles clear early on in the sentence, and thus a syntactic reanalysis was not required.

The neural correlates of semantic processing for iconic co-speech gestures seems quite similar to that of spoken words and manual signs, as indexed by the N400 ERP component. In addition, the temporal overlap of gestures with speech modulates their semantic processing, thus corroborating the dependence of co-speech gestures on the speech channel (in contrast to signs that are not dependent on another system). Furthermore, gestures (beats) can influence syntactic processing of an utterance, as indexed by modulations of the P600 ERP component.

Co-speech gesture comprehension: Functional MRI studies

Functional MRI studies have attempted to locate the brain areas involved in the perception of iconic gestures in relation to speech. In general, these studies found left frontal and left posterior temporal cortices to be implicated in interpreting gestures and/or integrating gestures with speech, more specifically the left IFG, posterior superior temporal sulcus (STSp), and bilateral MTG (e.g., Dick, Mok, Raja Beharelle, Goldin-Meadow, & Small, 2012; Straube, Weis, Green, & Kircher, 2012; Willems, Özyürek, & Hagoort, 2007, 2009). Interestingly, studies examining spoken language comprehension alone have also found that increased semantic processing results in increased activity in these regions, especially left IFG and MTG (e.g., Snijders et al., 2009).

The contribution of left IFG to semantic integration of speech and gesture was first reported by Willems et al. (2007). Participants heard sentences in which a critical word was accompanied by a gesture (same stimuli from Özyürek et al., 2007). Either the word or the gesture could be semantically anomalous (i.e., incongruent) with respect to the context set up by the sentence. The incongruent word or gesture (demanding more semantic processing) elicited greater activity than congruent conditions in left IFG.

Left IFG has also been found to respond more strongly to metaphoric gestures, that is, gestures with abstract meaning (e.g., a "high" gesture accompanying speech like "the level of presentation was high"), compared to iconic gestures accompanying the same speech (Kircher et al., 2009). Dick et al. (2012) also found left IFG to be more active for complementary gestures (speech: "work"; gesture: typing) than for redundant gestures (speech: "typing"; gesture: typing). Complementary

gestures, like metaphoric gestures, add information and require more semantic processing than redundant gestures. Finally, Skipper, Goldin-Meadow, Nusbaum, and Small (2009) showed that when iconic gestures were related to the accompanying speech, they exhibited a weaker influence on other motor and language-relevant cortical areas (including left IFG) compared to when the hand movements were meaningless (i.e., grooming gestures) or when there were no hand movements.

Thus, left IFG is responsive to iconic gestures, especially to those with an increased semantic processing load, that is, when gestures are difficult to integrate into the previous or overlapping co-speech context (i.e., incongruent, metaphoric, or complementary iconic gestures).

Posterior temporal regions are also involved in the semantic integration of gesture and speech. While MTG is more frequently found to be involved in semantic integration of speech and gesture, the role of STS has been more controversial. Holle et al. (2008) suggested that activity in STSp reflects sensitivity to the semantic integration of gesture and speech. In that study, STSp (but not left IFG) was more active for speech (dominant or subordinate homonyms) accompanied by meaningful iconic gestures than to speech accompanied by nonmeaningful grooming movements. However, Dick et al. (2012) and Willems et al. (2007, 2009) did not find activation in this area. Dick et al. (2012) argued that STSp may be involved in connecting information from the visual and auditory modalities in general, but not in semantic integration per se.

A stronger consensus has been achieved with regard to activation of left and/or right posterior MTG (MRTp). Green et al. (2009) found that left MTGp responded more strongly to sentences accompanied by unrelated gestures (hard to make sense of in relation to speech) than to those accompanied by related gestures. Dick et al. (2012) also found this area to be sensitive to complementary gestures, in comparison to redundant gestures. Willems et al. (2009) found that the left and right MTGp responded more to speech accompanied by incongruent pantomimes (conventionalized actions with objects such as ironing or twisting-the meaning of which would be clear without speech) than to the same speech accompanied by congruent pantomimes. However, MTGp was not activated for incongruent pairs of speech and co-speech gestures (these gestures would be ambiguous without speech) compared to congruent pairs. Incongruent speech-gesture pairs activated only left IFG and not MTGp. The authors argued that bilateral MTG is more likely to be involved in matching two input streams for which there

is a relatively stable common object representation (i.e., "twist" in speech with a twisting gesture), parallel to the notion that both the sight of a dog and the sound of its barking form part of a representation of our knowledge about dogs (Hein et al., 2007). However, when integration of gesture and speech requires a new representation of the input streams, the increased semantic processing of iconic gestures results in increased activation of left IFG. At this point, these characterizations should be seen more as tendencies rather than exclusive functions of left IFG and MTG in speech and gesture integration.

Straube et al. (2012) attempted to isolate brain activation for iconic gestures (regardless of their involvement in speech integration). They compared activation for meaningful spoken sentences (S+) to sentences from an unknown language (S-), and they also compared activation for co-speech gestures presented without their accompanying speech (G+) with meaningless gestures (G-). Meaningful iconic gestures activated left IFG, bilateral parietal cortex, and bilateral temporal areas, but the overlap of activations for meaningful speech and meaningful gestures occurred in left IFG and bilateral MTG. These findings are consistent with the hypothesis by Xu et al. (2009) that left IFG and MTGp are involved in meaning extraction for communicative gestures (with or without speech) as well as for speech alone.

Functional MRI studies on semantic comprehension of co-speech iconic gestures and their integration indicate a similar neural signature to that for the semantic comprehension of words in context: a critical role for left IFG (sensitive to the increase in the semantic load required to process iconic gestures) and MTG (activated when similar information is conveyed in the two input streams). STG and STS may be engaged in the integration of gesture and speech at the audio-visual level, in addition to playing a possible role in meaning integration.

Conclusion

This review has revealed a surprising degree of overlap between the cortical regions and processes that support both signed and spoken language and co-speech gesture processing, in spite of the differences in their properties at many levels. Even though less is known for co-speech gesture production than for sign, the existing evidence suggests left-hemisphere dominance for the production of sign, gesture, and speech. However, both sign and gesture seem to involve the right hemisphere for some types of representations. Furthermore, for both speech and sign, left IFG is involved in lexical

production, despite differences in the articulators. Left superior parietal cortex seems to be critically involved in sign language production, possibly due to the articulatory demands of manual phonology and somatosensory output monitoring.

Regarding comprehension, evidence from ERP studies indicates that the N400 response indexes semantic processing for both language modalities. The integration of meaningful information appears to follow the same time course for signs and words within a sentence context and for gestures in a speech context. In addition, the P600 component is sensitive to syntactic violations in signed and spoken languages, and this response can be mitigated by the presence of a co-speech gesture that reduces the need for syntactic reanalysis. Evidence from fMRI indicates a role for posterior superior temporal cortex in comprehending co-speech gesture and sign language, although the precise function of this region is likely to be different for the two. For sign language, STG/STS may be more engaged in phonological and lexical decoding of manual signs, whereas for co-speech gesture, STG/STS may be involved in audio-visual integration. Finally, both left IFG and MTG are engaged in semantic processing for language (both spoken and signed) and for iconic co-speech gestures.

The commonalities in the brain's processing of communicative information from co-speech gesture and sign (and in many ways speech) are striking, in spite of the differences in modalities (e.g., gesture is dependent on speech, but sign language is unimodal) and differences in the categorical versus gradient nature of representations. These commonalities underscore the fact that the brain's general infrastructure for language and communication can be recruited by different formats through which communicative information is transmitted.

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