Neural systems supporting linguistic structure, linguistic experience, and symbolic communication in sign language and gesture

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Sign languages used by deaf communities around the world possess the same structural and organizational properties as spoken languages: In particular, they are richly expressive and also tightly grammatically constrained. They therefore offer the opportunity to investigate the extent to which the neural organization for language is modality independent, as well as to identify ways in which modality influences this organization. The fact that sign languages share the visual–manual modality with a nonlinguistic symbolic communicative system—gesture—further allows us to investigate where the boundaries lie between language and symbolic communication more generally. In the present study, we had three goals: to investigate the neural processing of linguistic structure in American Sign Language (using verbs of motion classifier constructions, which may lie at the boundary between language and gesture); to determine whether we could dissociate the brain systems involved in deriving meaning from symbolic communication (including both language and gesture) from those specifically engaged by linguistically structured content (sign language); and to assess whether sign language experience influences the neural systems used for understanding nonlinguistic gesture. The results demonstrated that even sign language constructions that appear on the surface to be similar to gesture are processed within the left-lateralized frontal-temporal network used for spoken languages—supporting claims that these constructions are linguistically structured. Moreover, although nonsigners engage regions involved in human action perception to process communicative, symbolic gestures, signers instead engage parts of the language-processing network—demonstrating an influence of experience on the perception of nonlinguistic stimuli.

brain | American Sign Language | fMRI | deafness | neuroplasticity

Sign languages such as American Sign Language (ASL) are natural human languages with linguistic structure. Signed and spoken languages also largely share the same neural substrates, including left hemisphere dominance revealed by brain injury and neuroimaging. At the same time, sign languages provide a unique opportunity to explore the boundaries of what, exactly, "language" is. Speech-accompanying gesture is universal (1), yet such gestures are not language—they do not have a set of structural components or combinatorial rules and cannot be used on their own to reliably convey information. Thus, gesture and sign language are qualitatively different, yet both convey symbolic meaning via the hands. Comparing them can help identify the boundaries between language and nonlinguistic symbolic communication.

Despite this apparently clear distinction between sign language and gesture, some researchers have emphasized their apparent similarities. One construction that has been a focus of contention is "classifier constructions" (also called "verbs of motion"). In ASL, a verb of motion (e.g., moving in a circle) will include a root expressing the motion event, morphemes marking the manner and direction of motion (e.g., forward or backward), and also a classifier that specifies the semantic category (e.g., vehicle) or size and shape (e.g., round, flat) of the object that is moving (2). Although verbs of motion with classifiers occur in some spoken languages, in ASL these constructions are often iconic—the forms of the morphemes are frequently similar to the visual–spatial meanings they express—and they have therefore become a focus of discussion about the degree to which they (and other parts of ASL) are linguistic or gestural in character. Some researchers have argued that the features of motion and spatial relationships marked in ASL verbs of motion are in fact not linguistic morphemes but are based on the analog imagery system that underlies nonlinguistic visual–spatial processing (3–5). In contrast, Supalla (2, 6, 7) and others have argued that these ASL constructions are linguistic in nature, differing from gestures in that they have segmental structure, are produced and perceived in a discrete categorical (rather than analog) manner, and are governed by morphological and syntactic regularities found in other languages of the world.

These similarities and contrasts between sign language and gesture allow us to ask some important questions about the neural systems for language and gesture. The goal of this study was to examine the neural systems underlying the processing of ASL verbs of motion compared with nonlinguistic gesture. This allowed us to ask whether, from the point of view of neural systems, there is

Significance

Although sign languages and nonlinguistic gesture use the same modalities, only sign languages have established vocabularies and follow grammatical principles. This is the first study (to our knowledge) to ask how the brain systems engaged by sign language differ from those used for nonlinguistic gesture matched in content, using appropriate visual controls. Signers engaged classic left-lateralized language centers when viewing both sign language and gesture; nonsigners showed activation only in areas attuned to human movement, indicating that sign language experience influences gesture perception. In signers, sign language activated left hemisphere language areas more strongly than gestural sequences. Thus, sign language constructions—even those similar to gesture—engage language-related brain systems and are not processed in the same ways that nonsigners interpret gesture.

"linguistic structure" in ASL verbs of motion. It also allowed us to distinguish networks involved in "symbolic communication" from those involved specifically in language, and to determine whether "sign language experience" alters systems for gesture comprehension.

It is already established that a very similar, left-lateralized neural network is involved in the processing of many aspects of lexical and syntactic information in both spoken and signed languages. This includes the inferior frontal gyrus (IFG) (classically called Broca's area), superior temporal sulcus (STS) and adjacent superior and middle temporal gyri, and the inferior parietal lobe (IPL) (classically called Wernicke's area) including the angular (AG) and supramarginal gyri (SMG) (4, 8–18). Likewise, narrative and discourse-level aspects of signed language depend largely on right STS regions, as they do for spoken language (17, 19).

Although the neural networks engaged by signed and spoken language are overall quite similar, some studies have suggested that the linguistic use of space in sign language engages additional brain regions. During both comprehension and production of spatial relationships in sign language, the superior parietal lobule (SPL) is activated bilaterally (4, 5, 12). In contrast, parallel studies in spoken languages have found no (12) or only left (20) parietal activation when people describe spatial relationships. These differences between signed and spoken language led Emmorey et al. (5) to conclude that, "the location and movements within [classifier] constructions are not categorical morphemes that are selected and retrieved via left hemisphere language regions" (p. 531). However, in these studies, signers had to move their hands whereas speakers did not; it is unclear whether parietal regions are involved in processing linguistic structure in sign language as opposed to simply using the hands to symbolically represent spatial structure and relationships. Other studies have touched on the question of symbolic communication, comparing the comprehension of sign language with pantomime and with meaningless, sign-like gestures (11, 21–23). In signers, activation for both sign language and pantomime gestures was reported in classical language-related areas including the IFG, the posterior region of the STS (STSp), and the SMG, although typically these activations are stronger for sign language than gesture. Similar patterns of activation—although often more bilateral—have been observed in nonsigners, for meaningful as well as for meaningless gesture perception (24–27).

Thus, on the one hand, the classical left-lateralized "language-processing" network appears to be engaged by both signers and nonsigners for interpreting both sign language and nonlinguistic gesture. On the other hand, sign language experience appears to drive a specialization of these regions for signs over nonsigns in signers, whereas similar levels of activation are seen for gestures and spoken descriptions of human actions in nonsigners (27). In the right hemisphere, when viewing gestures both signers and nonsigners show activation of the homologs of the left hemisphere language regions noted above, including the STS (the STSp associated with biological motion, as well as more anterior areas), inferior and superior parietal regions, and the IFG.

One important caveat in considering the literature is that most studies have compared task-related activation to a simple baseline condition that did not control for the types of movements made or for other low-level stimulus features. Thus, apparent differences between sign language and gesture may in fact be attributable to their distinct physical/perceptual qualities, whereas subtle but important activation differences between sign language and nonlinguistic communication may have been "washed out" by the overall similarity of brain activation when people attempt to find meaning in hand, body, and face movement relative to a static stimulus.

Our goal in the present study was to further investigate the neural processing of ASL verbs of motion and to determine whether we could dissociate the brain systems involved in deriving meaning from "symbolic communication" (including both language

and gesture) from those specifically engaged by "linguistically structured content" (sign language), while controlling for the sensory and spatial processing demands of the stimuli. We also asked whether sign language experience influences the brain systems used to understand nonlinguistic gesture. To address these questions, we measured brain activation using functional MRI (fMRI) while two groups of people, deaf native ASL signers and nonsigning, hearing native English speakers, viewed two types of videos: ASL verbs of motion constructions describing the paths and manners of movement of toys [e.g., a toy cow falling off a toy truck, as the truck moves forward (2); see Fig. S5 for examples], and gestured descriptions of the same events. Importantly, we also included a "backward-layered" control condition in which the ASL and gesture videos were played backward, with three different videos superimposed (as in refs. 17 and 18).

We predicted that symbolic communication (i.e., both gesture and ASL, in signers and nonsigners) would activate areas typically seen in both sign language and meaningful gesture processing, including the left IFG and the SMG and STSp bilaterally. We further predicted that the left IFG would show stronger activation for linguistically structured content, i.e., in the contrast of ASL versus gesture in signers but not in nonsigners. We also predicted that other areas typically associated with syntactic processing and lexical retrieval, including anterior and middle left STS, would be more strongly activated by ASL in signers. Such a finding would provide evidence in favor of the argument that verbs of motion constructions are governed by linguistic morphology and argue against these being gestural constructions rather than linguistic. We further predicted that visual–manual language experience would lead to greater activation of the left IFG of signers than nonsigners when viewing gesture, although less than for ASL.

Results

Behavioral Performance. Overall, deaf signers showed greater accuracy than hearing nonsigners in judging which picture matched the preceding video, shown in Fig. S1. Deaf signers were more accurate than nonsigners for both ASL (signers: 1.99% errors; nonsigners: 17.85% errors) and for gestures (signers: 2.37% errors; nonsigners: 5.68% errors). A generalized linear mixed model fitted using a binomial distribution, involving factors Group (signers, nonsigners) and Stimulus Type (ASL, gesture) identified a Group × Stimulus Type interaction ($z = 3.53$; $P = 0.0004$). Post hoc tests showed that signers were significantly more accurate than hearing nonsigners for both ASL ($z = 7.61$; $P < 0.0001$) and for gestures ($z = 2.9$; $P = 0.004$). Furthermore, deaf signers showed similar levels of accuracy on both ASL and gesture stimuli, whereas hearing nonsigners were significantly more accurate in judging gestural than ASL stimuli ($z = 6.91$; $P < 0.0001$).

Examination of the reaction times (RTs) shown in Fig. S1 suggested an interaction between Group and Stimulus Type for this measure as well, with signers showing faster responses to ASL (1,543.4 ms; SD = 264.1) than to gestures (1,815.4 ms; SD = 314.3), but nonsigners showing faster responses to gestures (1,701.3 ms; SD = 325.3) than to ASL (1,875.0 ms; SD = 334.4). This observation was borne out by the results of a 2 (Group) × 2 (Stimulus Type) linear mixed-effects analysis, which included a significant Group × Stimulus Type interaction [$F_{(1,2,795)} = 148.08$; $P < 0.0001$]. RTs were significantly faster for signers than nonsigners when judging ASL stimuli ($t = 3.36$; $P = 0.0006$); however, the two groups did not differ significantly when judging gesture stimuli ($t = 1.15$; $P = 0.2493$). Signers were also significantly faster at making judgments for ASL than gesture stimuli ($t = 10.54$; $P < 0.0001$), whereas nonsigners showed the reverse pattern, responding more quickly gesture stimuli ($t = 6.63$; $P < 0.0001$).

fMRI Data. Although we developed backward-layered control stimuli to closely match and control for the low-level properties of our stimuli, we first examined the contrast with fixation to compare our

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data with previous studies (most of which used this contrast) and to gain perspective on the entire network of brain regions that responded to ASL and gesture. This is shown in Fig. S2 with details in Tables S1 and S2. Relative to fixation, ASL and gesture activated a common, bilateral network of brain regions in both deaf signers and hearing nonsigners, including occipital, temporal, inferior parietal, and motor regions. Deaf signers showed unique activation in the IFG and the anterior and middle STS bilaterally.

Contrasts with Backward-Layered Control Stimuli. The better-matched contrasts of ASL and gesture with backward-layered control stimuli identified a subset of the brain regions activated in the contrast with fixation, as seen in Fig. 1. Details of activation foci are provided in Tables S3 and S4. Very little of this activation was shared between signers and nonsigners. Notably, all of the activation in the occipital and superior parietal lobes noted in the contrast with fixation baseline was eliminated when we used a control condition that was matched on higher-level visual features. On the lateral surface of the cortex, activations were restricted to areas in and around the IFG and along the STS, extending into the IPL. Medially, activation was found in the ventromedial frontal cortex and fusiform gyrus for both groups, for ASL only. Signers uniquely showed activation in the left IFG and bilateral anterior/middle STS, for both ASL and gesture. Nonsigners uniquely showed activation bilaterally in the STSp for both ASL and gesture (although with a small amount of overlap with signers in the left STSp), as well as in the left inferior frontal sulcus and right IFG for ASL only. The only area showing any extensive overlap between signers and nonsigners was the right STS.

Comparison of ASL and Gesture Within Each Group. No areas were more strongly activated by gesture than by ASL in either group. In signers, the ASL–gesture contrast yielded an exclusively left-lateralized network, including the IFG and middle STS, as well as the fusiform gyrus (Fig. 2, *Left*, and Table S5). By contrast, the only areas that showed significantly stronger activation for ASL than gesture in hearing people was a small part of the left STSp (distinct from the areas activated in signers) and the posterior cingulate gyrus. Although nonsigners showed significant activation for ASL but not gesture in or around the IFG bilaterally, these activations were not significantly stronger for ASL than for gesture, implicating subthreshold activation for gesture. Between-condition contrasts for the data relative to fixation baseline (without the backward-layered control condition subtracted) are shown in Fig. S3.

Between-Group Comparisons. Signers showed significantly stronger activation for ASL than nonsigners in the anterior/middle STS bilaterally and in the left IFG (Fig. 2, *Right*, and Table S6). The area of stronger activation in the left IFG did not survive multiple-comparison correction. However, because differences between groups were predicted a priori in this region, we interrogated it using a post hoc region of interest analysis. Left IFG was defined as Brodmann's areas 44 and 45 (28), and within this we thresholded activations at $z > 2.3$, uncorrected for multiple comparisons. As seen in Fig. 2, the area that showed stronger activation for signers than nonsigners was within the left IFG cluster that, in signers, showed stronger activation for ASL than gesture. Hearing nonsigners showed greater activation than signers only for gesture, and this was restricted to the STSp/SMG of the right hemisphere. Between-group contrasts for the data relative to fixation baseline (without the backward-layered control condition subtracted) are shown in Fig. S4.

Discussion

The central question of this study was whether distinct brain systems are engaged during the perception of sign language, compared with gestures that also use the visual–manual modality and are symbolic communication but lack linguistic structure. Some previous work has suggested that aspects of sign language—such as verbs of motion—are nonlinguistic and are processed like gesture, thus relying on brain areas involved in processing biological motion and other spatial information. This position would predict shared brain systems for understanding verbs of motion constructions and nonlinguistic gestures expressing similar content. In contrast, we hypothesized that verbs of motion constructions are linguistically governed and, as such, would engage language-specific brain systems in signers distinct from those used for processing gesture. We also investigated whether knowing sign language influenced the neural systems recruited for nonlinguistic gesture, by comparing responses to gesture in signers and nonsigners. Finally, we compared signers and nonsigners to determine whether understanding symbolic communication differs when it employs a linguistic code as opposed to when it is created ad hoc. Because there is little symbolic but nonlinguistic communication in the oral–aural channel, such a comparison is best done using sign language and gesture. Although many neuroimaging studies have contrasted language with control stimuli, to our knowledge no studies have compared linguistic and nonlinguistic stimuli while attempting to match the semantic and symbolic content. Here, ASL and gesture were each used to describe the same action events.
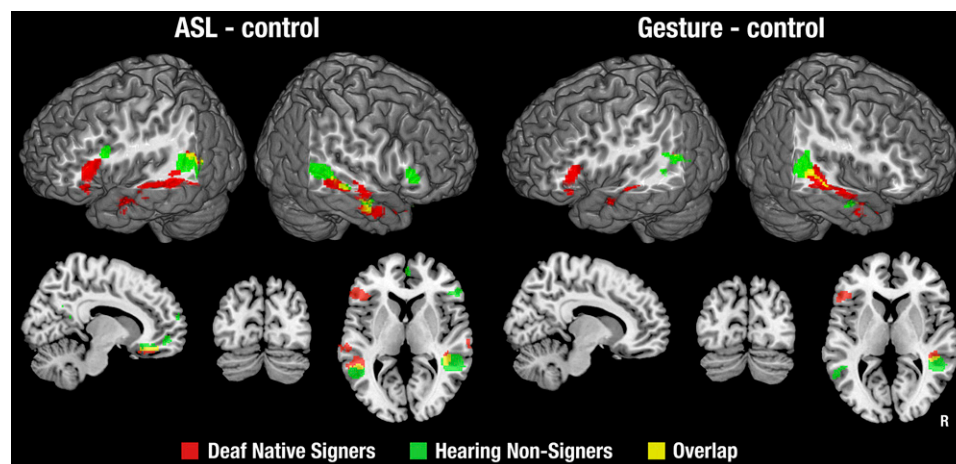
Fig. 1. Statistical maps for each stimulus type relative to the backward-layered control stimuli, in each subject group. Statistical maps were masked with the maps shown in Fig. S2, so that all contrasts represent brain areas activated relative to fixation baseline. Thresholded at $z > 2.3$, with a cluster size-corrected $P < 0.05$. In the coronal and sagittal views, the right side of the brain is shown on the right side of each image.
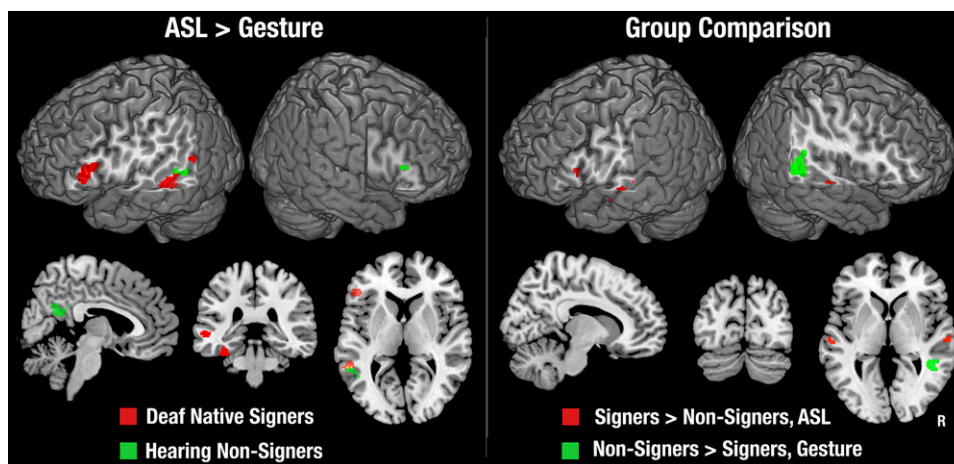
Fig. 2. (*Left*) Between-condition differences for each subject group, for the contrasts with backward-layered control stimuli. No areas showed greater activation for gesture than ASL in either group. Thresholded at $z > 2.3$, with a cluster size-corrected $P < 0.05$. (*Right*) Between-group differences for the contrast of each stimulus type relative to the backward-layered control stimuli. No areas were found that showed stronger activation in signers than nonsigners for gesture, nor in nonsigners than signers for ASL. Thresholded at $z > 2.3$, with a cluster size-corrected $P < 0.05$. Significant between-group differences in the left IFG were obtained in a planned region of interest analysis at $z > 2.3$, uncorrected for cluster size.

In the present study, compared with the low-level fixation baseline, ASL and gesture activated an extensive, bilateral network of brain regions in both deaf signers and hearing nonsigners. This network is consistent with previous studies of both sign language and gesture that used similar contrasts with a low-level baseline (10, 22–27). Critically, however, compared with the backward-layered conditions that controlled for stimulus features (such as biological motion and face perception) and for motor responses, a much more restricted set of brain areas was activated, with considerably less overlap across groups and conditions. Indeed, the only area commonly activated across sign language and gesture in both signers and nonsigners was in the middle/anterior STS region of the right hemisphere. In general, when there were differences between stimulus types, ASL elicited stronger brain activation than gesture in both groups. However, the areas that responded more strongly to ASL were almost entirely different between groups, again supporting the influence of linguistic experience in driving the brain responses to symbolic communication.

Linguistic Structure. Our results show that ASL verbs of motion produce a distinct set of activations in native signers, based in the classic left hemisphere language areas: the IFG and anterior/middle STS. This pattern of activation was significantly different from that found in signers observing gesture sequences expressing approximately the same semantic content, and was wholly different from the bilateral pattern of activation in the STSp found in hearing nonsigners observing either sign language or gestural stimuli. These results thus suggest that ASL verbs of motion are not processed by native signers as nonlinguistic imagery—because nonsigners showed activation primarily in areas associated with general biological motion processing—but rather are processed in terms of their linguistic structure (i.e., as complex morphology), as Supalla (2, 6, 7) has argued. This finding is also consistent with evidence that both grammatical judgment ability and left IFG activation correlated with age of acquisition in congenitally deaf people who learned ASL as a first language (14). Apparently, despite their apparent iconicity, ASL verbs of motion are processed in terms of their discrete combinatorial structure, like complex words in other languages, and depend for this type of processing on the left hemisphere network that underlies spoken as well as other aspects of signed languages.

The other areas more strongly activated by ASL—suggesting linguistic specialization—were in the left temporal lobe. These

included the middle STS—an area associated with lexical (lemma) selection and retrieval in studies of spoken languages (29)—and the posterior STS. For signers, this left-lateralized activation was posterior to the STSp region activated bilaterally in nonsigners for both ASL and gesture and typically associated with biological motion processing. The area activated in signers is in line with the characterization of this region as "Wernicke's area" and its association with semantic and phonological processing.

Symbolic Communication. Symbolic communication was a common feature of both the ASL and gesture stimuli. Previous studies had suggested that both gesture and sign language engage a broad, common network of brain regions including classical left hemisphere language areas. Some previous studies used pantomimed actions (10, 21, 27), which are more literal and less abstractly symbolic than some of the gestures used in the present study; other studies used gestures with established meanings [emblems (22, 27, 30)], or meaningless gestures (21, 23, 30). Thus, the stimuli differed from those in the present study in terms of their meaningfulness and degree of abstract symbolism. Our data revealed that, when sign language and gesture stimuli are closely matched for content, and once perceptual contributions are properly accounted for, a much more restricted set of brain regions are commonly engaged across stimulus types and groups—restricted to middle and anterior regions of the right STS. We have consistently observed activation in this anterior/middle right STS area in our previous studies of sign language processing, in both hearing native signers and late learners (16) and in deaf native signers both for ASL sentences with complex morphology [including spatial morphology (18), and narrative and prosodic markers (17)]. The present findings extend this to nonlinguistic stimuli in nonsigners, suggesting that the right anterior STS is involved in the comprehension of symbolic manual communication regardless of linguistic structure or sign language experience.

Sign Language Experience. Our results indicate that lifelong use of a visual–manual language alters the neural response to nonlinguistic manual gesture. Left frontal and temporal language processing regions showed activation in response to gesture only in signers, once low-level stimulus features were accounted for. Although these same left hemisphere regions were more strongly activated by ASL, their activation by gesture exclusively in signers suggests that sign language experience drives these areas to

attempt to analyze visual–manual symbolic communication even when it lacks linguistic structure. An extensive portion of the right anterior/middle STS was also activated exclusively in signers. This region showed no specialization for linguistically structured material, although in previous studies we found sensitivity of this area to both morphological and narrative/prosodic structure in ASL (17, 18). It thus seems that knowledge of a visual–manual sign language can lead to this region's becoming more sensitive to manual movements that have symbolic content, whether linguistic or not, and that activation in this region increases with the amount of information that needs to be integrated to derive meaning.

It is interesting to note that our findings contrast with some previous studies that compared ASL and gesture, and found left IFG activation only for ASL (10, 21). This finding was interpreted as evidence for a "gating mechanism" whereby signs were distinguished from gesture at an early stage of processing in native signers, with only signs passed forward to the IFG. However, those previous studies did not use perceptually matched control conditions (allowing for the possibility of stimulus feature differences) and used pantomimed actions. In contrast, we used sequences of gestures that involved the articulators to symbolically represent objects and their paths. In this sense, our stimuli more closely match the abstract, symbolic nature of language than does pantomime. Thus, there does not appear to be a strict "gate" whereby the presence or absence of phonological or syntactic structure determines whether signers engage the left IFG; rather signers may engage language-related processing strategies when meaning needs to be derived from abstract symbolic, manual representations.

Conclusions

This study was designed to assess the effects of linguistic structure, symbolic communication, and linguistic experience on brain activation. In particular, we sought to compare how sign languages and nonlinguistic gesture are treated by the brain, in signers and nonsigners. This comparison is of special interest in light of recent claims that some highly spatial aspects of sign languages (e.g., verbs of motion) are organized and processed like gesture rather than like language. Our results indicate that ASL verbs of motion are not processed like spatial imagery or other nonlinguistic materials, but rather are organized and mentally processed like grammatically structured language, in specialized brain areas including the IFG and STS of the left hemisphere.

Although in this study both ASL and gesture conveyed information to both signers and nonsigners, we identified only restricted areas of the right anterior/middle STS that responded similarly to symbolic communication across stimulus types and groups. Overall, our results suggest that sign language experience modifies the neural networks that are engaged when people try to make sense of nonlinguistic, symbolic communication. Nonsigners engaged a bilateral network typically engaged in the perception of biological motion. For native signers, on the other hand, rather than sign language being processed like gesture, gesture is processed more like language. Signers recruited primarily language-processing areas, suggesting that lifelong sign language experience leads to imposing a language-like analysis even for gestures that are immediately recognized as nonlinguistic.

Finally, our findings support the analysis of verbs of motion classifier constructions as being linguistically structured (2, 6, 7), in that they specifically engage classical left hemisphere language-processing regions in native signers but not areas subserving nonlinguistic spatial perception. We suggest that this is because, although the signs for describing spatial information may have had their origins in gesture, over generations of use they have become regularized and abstracted into segmental, grammatically controlled linguistic units—a phenomenon that has been repeatedly described in the development and evolution of sign languages (31–33) and the structure and historical emergence of full-fledged adult sign languages (2, 6, 7, 34). Human communication systems seem always to move toward becoming rapid, combinatorial, and highly grammaticized systems (31); the present findings suggest that part of this change may involve recruiting the left hemisphere network as the substrate of rapid, rule-governed computation.

Materials and Methods

Please see *SI Materials and Methods* for detailed materials and methods.

Participants. Nineteen congenitally deaf native learners of ASL (signers) and 19 normally hearing, native English speakers (nonsigners) participated. All provided informed consent. Study procedures were reviewed by the University of Rochester Research Subjects Review Board.

ASL and Gesture Stimuli. Neural activation to sign language compared with gesture was observed by asking participants to watch videotaped ASL and gesture sequences expressing approximately the same content. Both ASL and gesture video sequences were elicited by the same set of stimuli, depicting events of motion. These stimuli included a set of short videos of toys moving along various paths, relative to other objects, and a set of line drawings depicting people, animals, and/or objects engaged in simple activities. Examples of these are shown in Fig. S5. After viewing each such video, the signer or gesturer was filmed producing, respectively, ASL sentences or gesture sequences describing the video. These short clips were shown to participants in the scanner. The ASL constructions were produced by a native ASL signer; gestured descriptions were produced by three native English speakers who did not know sign language. The native signer and the gesturers were instructed to describe each video or picture without speaking, immediately after viewing it. The elicited ASL and gestures were video recorded, edited, and saved as digital files for use in the fMRI experiment. Backward-layered control stimuli were created by making the signed and gestured movies partly transparent, reversing them in time, and then overlaying three such movies (all of one type, i.e., ASL or gesture) in software and saving these as new videos.

fMRI Procedure. Each participant completed four fMRI scans (runs) of 40 trials each. Each trial consisted of a task cue (instructions to try to determine the meaning of the video, or watch for symmetry between the two hands), followed by a video (ASL, gesture, or control), followed by a response prompt. For ASL and gesture movies, participants saw two pictures and had to indicate via button press which best matched the preceding video. For control movies, participants made button presses indicating whether, during the movie, three hands had simultaneously had the same handshape. Two runs involved ASL stimuli only, whereas the other two involved gesture stimuli only. Within each run, one-half of the trials were the ASL or gesture videos and the other half were their backward-layered control videos. The ASL movies possessed enough iconicity, and the "foil" pictures were designed to be different enough from the targets that task performance was reasonably high even for nonsigners viewing ASL. Data were collected using an echo-planar imaging pulse sequence on a 3-T MRI system (echo time, 30 ms; repetition time, 2 s; 90° flip angle, 4-mm isotropic resolution). fMRI data were analyzed using FSL *FEAT* software according to recommendations of the software developers (fsl.fmrib.ox.ac.uk/fsl/fslwiki/).

1. McNeill D (1985) So you think gestures are nonverbal? *Psychol Rev* 92(3):350–371.
2. Supalla T (1982) Structure and acquisition of verbs of motion and location in American Sign Language. PhD thesis (University of California, San Diego).
3. Liddell SK (2003) *Grammar, Gesture, and Meaning in American Sign Language* (Cambridge Univ Press, Cambridge, UK).
4. Emmorey K, et al. (2002) Neural systems underlying spatial language in American Sign Language. *Neuroimage* 17(2):812–824.

5. Emmorey K, McCullough S, Mehta S, Ponto LLB, Grabowski TJ (2013) The biology of linguistic expression impacts neural correlates for spatial language. *J Cogn Neurosci* 25(4):517–533.

6. Supalla T (1990) Serial verbs of motion in ASL. *Theoretical Issues in Sign Language Research*, eds Fischer SD, Siple P (The Univ of Chicago Press, Chicago), pp 127–152.

7. Supalla T (2003) Revisiting visual analogy in ASL classifier predicates. *Perspectives on Classifier Constructions in Sign Language*, ed Emmorey K (Lawrence Erlbaum Associates, Mahwah, NJ), pp 249–257.

8. Bavelier D, et al. (2008) Encoding, rehearsal, and recall in signers and speakers: Shared network but differential engagement. *Cereb Cortex* 18(10):2263–2274.

9. Campbell R, MacSweeney M, Waters D (2008) Sign language and the brain: A review. *J Deaf Stud Deaf Educ* 13(1):3–20.

10. Corina D, et al. (2007) Neural correlates of human action observation in hearing and deaf subjects. *Brain Res* 1152:111–129.

11. Hickok G, Bellugi U, Klima ES (1996) The neurobiology of sign language and its implications for the neural basis of language. *Nature* 381(6584):699–702.

12. MacSweeney M, et al. (2002) Neural correlates of British sign language comprehension: Spatial processing demands of topographic language. *J Cogn Neurosci* 14(7): 1064–1075.

13. MacSweeney M, Capek CM, Campbell R, Woll B (2008) The signing brain: The neurobiology of sign language. *Trends Cogn Sci* 12(11):432–440.

14. Mayberry RI, Chen JK, Witcher P, Klein D (2011) Age of acquisition effects on the functional organization of language in the adult brain. *Brain Lang* 119(1):16–29.

15. Neville HJ, et al. (1998) Cerebral organization for language in deaf and hearing subjects: Biological constraints and effects of experience. *Proc Natl Acad Sci USA* 95(3):922–929.

16. Newman AJ, Bavelier D, Corina D, Jezzard P, Neville HJ (2002) A critical period for right hemisphere recruitment in American Sign Language processing. *Nat Neurosci* 5(1):76–80.

17. Newman AJ, Supalla T, Hauser PC, Newport EL, Bavelier D (2010) Prosodic and narrative processing in American Sign Language: An fMRI study. *Neuroimage* 52(2):669–676.

18. Newman AJ, Supalla T, Hauser P, Newport EL, Bavelier D (2010) Dissociating neural subsystems for grammar by contrasting word order and inflection. *Proc Natl Acad Sci USA* 107(16):7539–7544.

19. Hickok G, et al. (1999) Discourse deficits following right hemisphere damage in deaf signers. *Brain Lang* 66(2):233–248.

20. Damasio H, et al. (2001) Neural correlates of naming actions and of naming spatial relations. *Neuroimage* 13(6 Pt 1):1053–1064.

21. Emmorey K, Xu J, Gannon P, Goldin-Meadow S, Braun A (2010) CNS activation and regional connectivity during pantomime observation: No engagement of the mirror neuron system for deaf signers. *Neuroimage* 49(1):994–1005.

22. Husain FT, Patkin DJ, Thai-Van H, Braun AR, Horwitz B (2009) Distinguishing the processing of gestures from signs in deaf individuals: An fMRI study. *Brain Res* 1276: 140–150.

23. MacSweeney M, et al. (2004) Dissociating linguistic and nonlinguistic gestural communication in the brain. *Neuroimage* 22(4):1605–1618.

24. Decety J, et al. (1997) Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120(Pt 10):1763–1777.

25. Lotze M, et al. (2006) Differential cerebral activation during observation of expressive gestures and motor acts. *Neuropsychologia* 44(10):1787–1795.

26. Villarreal M, et al. (2008) The neural substrate of gesture recognition. *Neuropsychologia* 46(9):2371–2382.

27. Xu J, Gannon PJ, Emmorey K, Smith JF, Braun AR (2009) Symbolic gestures and spoken language are processed by a common neural system. *Proc Natl Acad Sci USA* 106(49): 20664–20669.

28. Eickhoff SB, et al. (2007) Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. *Neuroimage* 36(3):511–521.

29. Indefrey P (2011) The spatial and temporal signatures of word production components: A critical update. *Front Psychol* 2:255.

30. Husain FT, Patkin DJ, Kim J, Braun AR, Horwitz B (2012) Dissociating neural correlates of meaningful emblems from meaningless gestures in deaf signers and hearing non-signers. *Brain Res* 1478:24–35.

31. Newport EL (1981) Constraints on structure: Evidence from American Sign Language and language learning. *Minnesota Symposium on Child Psychology*, ed Collins, WA (Lawrence Erlbaum Associates, Hillsdale, NJ), Vol 14, pp 93–124.

32. Newport EL (1999) Reduced input in the acquisition of signed languages: Contributions to the study of creolization. *Language Creation and Language Change: Creolization, Diachrony, and Development*, ed DeGraff M (MIT Press, Cambridge, MA), pp 161–178.

33. Senghas A, Kita S, Ozyürek A (2004) Children creating core properties of language: Evidence from an emerging sign language in Nicaragua. *Science* 305(5691):1779–1782.

34. Supalla T, Clark P (2015) *Sign Language Archeology: Understanding the History and Evolution of American Sign Language* (Gallaudet Univ Press, Washington, DC).

35. Worsley KJ (2001) Statistical analysis of activation images. *Functional Magnetic Resonance Imaging: An Introduction to the Methods*, eds Jezzard P, Matthews PM, Smith SM (Oxford Univ Press, New York), pp 251–270.

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