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Motor-iconicity of sign language does not alter the neural systems underlying tool and action naming

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Abstract

Positron emission tomography was used to investigate whether the motor-iconic basis of certain forms in American Sign Language (ASL) partially alters the neural systems engaged during lexical retrieval. Most ASL nouns denoting tools and ASL verbs referring to tool-based actions are produced with a handshape representing the human hand holding a tool and with an iconic movement depicting canonical tool use, whereas the visual iconicity of animal signs is more idiosyncratic and inconsistent across signs. We investigated whether the motor-iconic relation between a sign and its referent alters the neural substrate for lexical retrieval in ASL. Ten deaf native ASL signers viewed photographs of tools/utensils or of actions performed with or without an implement and were asked to overtly produce the ASL sign for each object or action. The control task required subjects to judge the orientation of unknown faces. Compared to the control task, naming tools engaged left inferior and middle frontal gyri, bilateral parietal lobe, and posterior inferotemporal cortex. Naming actions performed with or without a tool engaged left inferior frontal gyrus, bilateral parietal lobe, and posterior middle temporal gyrus at the temporo-occipital junction (area MT). When motor-iconic verbs were compared with non-iconic verbs, no differences in neural activation were found. Overall, the results indicate that even when the form of a sign is indistinguishable from a pantomimic gesture, the neural systems underlying its production mirror those engaged when hearing speakers name tools or tool-based actions with speech.

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1. Introduction

Signed languages differ dramatically from spoken languages with respect to the articulators involved in language production. Signing involves movements of the hands and arms in space, whereas speaking involves movements of the tongue and lips in co-ordination with the vocal chords. The articulators required for signing are the same as those involved in non-linguistic reaching and grasping movements. However, unlike reaching and grasping, sign articulations are structured within a "phonological" system of contrasts (Stokoe, 1960). Like spoken languages, signed languages exhibit a sublexical level of structuring in which non-meaningful units are

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combined in a rule-governed fashion to form morphemes and words (for reviews, see Brentari, 1998; Corina & Sandler, 1993; Emmorey, 2002).

For grasping tasks, hand configuration is determined by the nature of the object to be held or manipulated. For sign production, hand configuration is determined by the phonological specification stored in the lexicon. For example, in American Sign Language (ASL) the hand configuration for the sign $APPLE^1$ is an "X" handshape (fist with index finger extended and bent), and this hand configuration contrasts with the handshape for CANDY (fist with the index finger extended

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¹ By convention, signs are represented by an upper-case English word that best represents the meaning of the sign. Multi-word glosses connected by hyphens are used when more than one English word is required to translate a single sign (e.g., BRUSH-HAIR).

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and straight). The signs APPLE and CANDY constitute a minimal pair, produced with the same movement (a twisting motion at the wrist) and at same location (at the side of the lower cheek), but they contrast in hand configuration. There is a limited inventory of contrasting hand configurations in ASL and this inventory differs from other signed languages. For example, Chinese Sign Language contains hand configurations that are not found in ASL, and vice versa. The hand configuration used to grasp objects is generally functionally determined, but the hand configuration for signs is dependent on the lexicon and phonology of a particular sign language (e.g., the signs for APPLE and CANDY in British Sign Language are formationally distinct from the corresponding ASL signs).

Although both signed and spoken languages exhibit a phonological level of structure, these languages differ with respect to the degree of iconicity exhibited by lexical forms (see Taub, 2001; for review and discussion). Spoken languages exhibit iconicity via sound symbolism, onomatopoeia, and temporal ordering (e.g., Hinton, Nichols, & Ohala, 1994). However, the auditory-vocal modality is an impoverished medium for creating iconic forms because most referents and actions have no associated auditory imagery and the vocal tract is limited in the types of sounds it can produce. In contrast, the visual-manual modality offers a rich resource for creating iconic form-meaning mappings and the lexicons of sign languages exhibit a high incidence of iconicity (see Pietrandrea, 2002).

The domain of iconicity that is relevant to the study reported here is the sensory-motoric iconicity observed in ASL "handling" verbs and in ASL nouns that refer to tools or manipulable objects. ASL signs that denote actions performed with an implement are generally expressed by handling classifier verbs in which the hand configuration depicts how the human hand holds and manipulates an instrument. For example, the sign BRUSH-HAIR is made with a grasping handshape and a "brushing" motion at the head (see Fig. 1A). Such verbs are referred to as *classifier* verbs because the handshape is morphemic and refers to a property of the referent object (e.g., the handle of a brush); see papers in Emmorey (2003) for a discussion of classifier constructions in signed languages. Handling classifier verbs are distinct from other classifier verb types because the



Fig. 1. Example sign responses when naming (A) actions performed with a tool (handling classifier verbs), (B) tools, and (C) actions performed without an implement (general verbs).

handshape depicts how someone holds the referent object, rather than representing the referent entity itself. For whole entity classifier verbs, such as CAR-MOVE-LEFTWARD, the handshape represents the referent object (the car), and the movement of the hand represents the referent's motion (the leftward motion of the car). In contrast, the movement of handling classifier verbs refers to the motion produced by an implied animate agent (e.g., a person brushing hair), rather than to the motion of the referent entity itself (in BRUSH-HAIR, the brush is not understood as moving of its own accord). As can be seen in Fig. 1A, the form of handling classifier verbs is quite iconic, depicting the hand configuration used to grasp and manipulate an object and the movement that is typically associated with the object's manipulation (e.g., brushing one's hair, bouncing a ball, or erasing a blackboard).

In addition, ASL nouns denoting tools or manipulable objects are often derived from instrument classifier verbs. For instrument classifier verbs, the object itself is represented by the articulator, and the movement of the sign reflects the stylized movement of the tool or implement. For example, the sign SCREWDRIVER shown in Fig. 1B is made with a twisting a motion, and the "H" handshape (fist with index and middle fingers extended) depicts the screwdriver itself, rather than how the hand would hold a screwdriver. In general, the movement of a noun in ASL reduplicates and shortens the movement of the related verb (Supalla & Newport, 1978). Thus, the twisting motion of the sign SCREW-DRIVER is repeated and relatively short. For some nouns, such as CUP shown in Fig. 1B, it is ambiguous whether the handshape depicts the object itself (a round cylinder) or how the hand grasps the object.

Given the motoric iconicity of handling classifier verbs and of many ASL nouns referring to manipulable objects, we investigated whether such iconicity impacts the neural systems that underlie tool and action naming for deaf ASL signers. In a previous PET study, we investigated naming animals with either ASL signs or with fingerspelled forms (Emmorey et al., 2003). Naming animals via fingerspelling does not involve an iconic relationship between form and meaning. However, naming animals with ASL signs often involves the production of visually iconic forms. For example, the sign TIGER is a bimanual sign produced with two "hooked 5" handshapes (all fingers extended and curved) that brush the sides of the face, as if tracing the stripes on the face of a tiger. The signs GIRAFFE and ELEPHANT involve iconic representations of the dominant physical features of these animals (i.e., the long neck of the giraffe and the trunk of the elephant are depicted by a tracing motion along the neck or out from the nose, respectively). While undergoing PET scanning, deaf ASL signers were presented with pictures of individual animals and asked to overtly sign or fingerspell the name of the animal. In the corresponding study by Damasio, Grabowski, Tranel, Hichwa, and Damasio (1996), English speakers named animals using overt speech.

The results indicated that naming animals with either iconic ASL signs or non-iconic English words activated mesial and ventral inferior temporal cortex in the left hemisphere (Damasio et al., 1996; Emmorey et al., 2003). We found no evidence that the iconicity of ASL signs for animals altered the neural systems involved in their production. When naming animals with ASL signs was directly contrasted with naming animals using (noniconic) fingerspelling, only minor differences in neural activity were found. Specifically, the production of fingerspelled forms activated supplementary motor areas, probably due to the increased motor planning and sequencing demanded by fingerspelling. In contrast, ASL signs activated portions of the left supramarginal gyrus, an area previously implicated in the retrieval of phonological features of ASL signs (Corina et al., 1999).

However, the sensory-motoric iconicity found in ASL handling classifier verbs and in ASL nouns denoting tools differs from the visually based iconicity found in ASL signs for animals. The iconicity of handling classifier verbs is relatively consistent, depicting canonical tool use. We predict that naming either tools or actions performed with a tool will engage cortical systems that are involved in object manipulation, specifically left premotor and left inferior parietal cortex. Activation in these regions is not predicted when signers name actions that are performed without an implement (e.g., YELL, READ, SLEEP; see Fig. 1C). However, activation in left premotor and left inferior parietal cortex when naming tools or tool-based actions would not be unique to sign language. Several studies have found activation in one or both of these regions for hearing speakers using picture naming or tool recognition tasks (Chao & Martin, 2000; Damasio et al., 2001; Grabowski, Damasio, & Damasio, 1998; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Okada et al., 2000).

For example, Grafton et al. (1997) found activation in left dorsal premotor cortex (BA 6) during tool naming and during tool-use naming (e.g., saying "to shave" when shown a razor). The authors hypothesize that movement schemas for using manipulable tools may be represented in dorsal premotor cortex adjacent to the hand/arm primary motor cortex, and these schemas may be automatically activated by the visual presentation of tools (see also Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). Grafton et al. (1997) suggest that this premotor activation "may subserve the motoric aspects of object semantics" (p. 235). In addition, viewing and naming tools selectively activates left inferior parietal cortex (BA 40) for hearing speakers (e.g., Chao & Martin, 2000; Damasio et al., 2001; Okada et al., 2000). Studies of patients with ideomotor apraxia and single-unit recording studies with non-human primates indicate that inferior parietal cortex plays an important role in matching the pattern of hand movements to the visuospatial characteristics of an object to be manipulated (e.g., Buxbuam, 2001; Sakata, Taira, Murata, & Mine, 1995). Thus, recognizing and naming tools with spoken language may recruit a left prefrontal-parietal network, which represents the visuospatial characteristics of hand movements that are associated with tools and commonly manipulated objects.

However, when hearing speakers are asked to pantomime tool-use gestures, an additional left parietal area is recruited, namely the superior parietal lobule (BA 7) (Choi et al., 2001; Johnson, Newman-Norlund, & Grafton, 2002; Moll et al., 2000). These studies all used a complex, but non-meaningful, sequence of hand movements as the baseline against which tool-use pantomimes were compared. Thus, the superior parietal lobule (SPL) appears to play an important role in the production of meaningful gestures related to object manipulation. Activation in SPL has not been reported when the subject's task is to recognize and/or name tools or manipulable objects. If the production of ASL handling classifier verbs or iconic signs for tools engages the same neural systems engaged when nonsigners produce pantomimic tool-use gestures, then we predict activation within the superior parietal lobule for tool and toolbased action naming by ASL signers.

In contrast, if the hand configurations and movements of ASL nouns denoting tools or of handling classifier verbs are part of a phonological representation (rather than of a pantomimic representation), then we predict that the production of these forms will pattern similarly to the production of ASL action verbs that do not exhibit sensory-motoric iconicity. In particular, we predict that naming tools or actions with ASL signs will engage the left inferior frontal gyrus, specifically Broca's area (BA 44/45). It has long been hypothesized that Broca's area is involved in phonological processing during speech production, and activation in the left inferior frontal gyrus (IFG) is generally found for picturenaming and almost always found for verb generation tasks (Indefrey & Levelt, 2000). Chao and Martin (2000) also report activation in left IFG for tool naming, but not when subjects simply recognized tools (during a viewing condition without naming). Furthermore, activation in left IFG has not been reported during tool-use pantomime (Choi et al., 2001; Moll et al., 2000).

In summary, we investigated whether the sensorymotoric iconicity of ASL signs for tools and for toolbased actions alters the neural systems that underlie lexical retrieval by comparing the production of these signs with the production of verbs that do not exhibit motoric iconicity (see Fig. 1). If the production of motorically iconic signs is akin to the production of pantomime, then activation should be observed in the left superior parietal lobule for these signs, but not for signs that have no pantomimic properties (i.e., "general verbs" that do not involve hand configurations or movements that depict object manipulation). If the motor-iconicity of ASL signs is irrelevant to lexical retrieval and these signs are simply treated as arbitrary lexical forms, then we should find activation within left inferior frontal gyrus, and there should be little or no difference in activation within left perisylvian cortices for the motorically iconic and the non-iconic signs. Finally, we hypothesize that naming tools and tool-based actions in ASL will engage a left prefrontal-parietal network, as has been found for English speakers when naming such actions and objects with non-iconic, arbitrary spoken words.

2. Methods

2.1. Subjects

Ten right-handed, adult native deaf signers were studied under a PET protocol using [¹⁵O]water. The subjects were 5 men and 5 women, aged 20–31, with 12 years or more of formal education and right-handed (handedness quotient of +90 or greater as measured by the Oldfield–Geschwind questionnaire). All had deaf parents and acquired ASL as their first language from birth. Nine subjects had a profound hearing loss (90 dB loss or greater), and one subject had a moderate hearing loss (60 dB loss). No subject had any history of neuro-logical or psychiatric disease. All gave formal consent in accordance with Federal and institutional guidelines.

2.2. Procedures

All subjects underwent MR scanning in a General Electric Signa scanner operating at 1.5T, using the following protocol: SPGR 30, TR 24, TE 7, NEX 1, FOV 24 cm, matrix 256×192 . Each of 3 individual 1NEX SPGR datasets was obtained with 124 contiguous coronal slices with thickness 1.5-1.7 mm and interpixel distance 0.94 mm. The slice thickness varied so as to be adjusted to the size of the brain and the head in order to sample the entire brain, while avoiding wrap artifacts. The three individual datasets were co-registered post hoc with Automated Image Registration (AIR 3.03) to produce a single data set, of enhanced quality, with pixel dimensions of 0.7 mm in plane and 1.5 mm between planes (Holmes et al., 1998). The MR sequences were reconstructed for each subject in 3-D using Brainvox (Damasio & Frank, 1992; Frank, Damasio, & Grabowski, 1997). Extracerebral voxels were edited away manually. The MR scans were used to confirm the absence of structural abnormalities, to plan the PET slice orientation, and to delineate regions of interest a priori.

PET-Brainvox (Grabowski et al., 1995; Damasio et al., 1994) was used to plan the PET slice orientation

parallel to the long axis of the temporal lobes. Talairach space was constructed directly for each subject via useridentification of the anterior and posterior commissures and the midsagittal plane in Brainvox. An automated planar search routine defined the bounding box and a piecewise linear transformation was used (Frank et al., 1997), as defined in the Talairach atlas (Talairach & Tournoux, 1988). After Talairach transformation, the MR datasets were warped (AIR 5th-order nonlinear algorithm) to an atlas space constructed by averaging 50 normal Talairach-transformed brains, rewarping each brain to the average, and finally averaging them again (analogous to the procedure described in Woods, Daprett, Sicotte, Toga, & Mazziotta, 1999). The Talairachtransformed 3D scans of all 10 subjects were averaged.

Each subject received 8 injections containing 50 mCi of [¹⁵O]water. Each subject performed 4 tasks, twice each. The tasks were the following: (1) production of names for tools and other manipulable objects; (2) production of names for actions performed with an implement; (3) production of names for actions performed without an implement; and (4) an orientation judgment performed on the faces of unknown persons

requiring the response YES if the face was in the canonic position (up) and NO if the face was inverted. Fig. 2 provides example picture stimuli from the target naming tasks (1) - (3).

For the control task (4), subjects made a signed response, but no naming was involved. This task was chosen as the baseline task because unknown faces do not evoke a name and yet depict real entities at least as complex as the stimuli presented in the other naming tasks, and it has been used in our previous word and sign retrieval experiments (Damasio et al., 1996, 2001; Emmorey et al., 2002, 2003). Using the same control task consistently allows us to explore the retrieval of words/signs for different conceptual categories and across separate subject groups. Following Damasio et al. (2001), the ISI for the tool and action naming tasks was 1.8 s (N = 20 per trial), and the ISI for the control task was 1.0 s (N = 36 per trial).

For all tasks, subjects responded with their right hand in a natural "whisper mode" so that the hand did not contact the face. One-handed signing is natural for whispering and also occurs during everyday signing (e.g., when one hand is occupied). Subjects' responses



Fig. 2. Example stimuli: (A) actions performed with a tool, (B) tools, and (C) actions performed without an implement.

were recorded during the PET study by a native ASL signer, and the responses were also videotaped for confirmation and later analysis. The stimuli were presented from 5 s after each injection (approximately 10 s before the bolus arrived in the brain) until 40 s after injection.

Positron emission tomography (PET) data were acquired with a General Electric 4096 Plus body tomograph (G.E. Medical Systems, Milwaukee, WI), yielding 15 transaxial slices with a nominal interslice interval of 6.5 mm. For each injection, 50 mCi of [15 O]water was administered as a bolus through a venous catheter. Arterial blood sampling was not performed.

Reconstructed images of the distribution of radioactive counts from each injection were coregistered with each other using Automated Image Registration (AIR 3.03, Roger Woods, UCLA). 3D MR and the mean coregistered PET data were also coregistered using PET-Brainvox and Automated Image Registration (AIR) (Woods, Mazziotta, & Cherry, 1993). PET data were Talairach-transformed as described above, masked to the coregistered MRI brain contour to exclude extracerebral voxels, and then smoothed with an isotropic 16 mm gaussian kernel by Fourier transformation, complex multiplication, and reverse Fourier transformation (Hichwa, Ponto, & Watkins, 1995). The final calculated image resolution was $18 \times 18 \times 18$ mm.

PET data were analyzed with a pixelwise linear model which estimated coefficients for global activity (covariable) and task and block/subject effects (classification variables) (Friston et al., 1995; Grabowski et al., 1996). We searched for increases in adjusted mean activity in images of t statistics generated for each of the planned contrasts. Critical t values were calculated using gaussian random field theory for t statistics (Worsley, 1994; Worsley, Evans, Marrett, & Neelin, 1992).

The planned contrasts were as follows:

- (a) To address the hypothesis that both naming tools and naming actions performed with a tool (handling classifier verbs) will engage left premotor, left inferior parietal cortex, and possibly Broca's area and/or left superior parietal cortex, the standard control task was subtracted from each naming task.
- (b) To address the hypothesis that naming actions performed without an implement (general verbs) will engage Broca's area, but not left premotor or parietal cortex, the standard control task was subtracted from naming actions performed without a tool.
- (c) To determine whether and how naming actions with handling classifier verbs differs from naming actions with general verbs that do not exhibit sensory-motoric iconicity, these tasks were subtracted from each other.
- (d) To determine whether and how naming actions performed with a tool differs from naming tools, these tasks were subtracted from each other.

3. Results

Response accuracy (percent correct) was high for all naming categories: 96.2% for actions performed without a tool (general verbs); 98.2% for actions performed with a tool (handling classifier verbs); and 99.2% for tools. In addition, handling classifier verbs were almost always produced in response to pictures of actions performed with a tool. Less than 3% of responses were non-classifier forms, e.g., producing the lexical verb CLEAN instead of the handling classifier verb SCRUB-BY-HAND. For pictures depicting actions performed without a tool, less than 2% of the responses were handling classifier verbs rather than general verbs, e.g., producing the handling classifier verb SWING-BY-HOLDING-ROPES (the handshape represents grasping) the ropes of a swing) instead of the general verb SWING (a "bent-H" handshape (middle and index fingers extended and bent) moves back and forth). Finally, less than 5% of the signed responses for pictures of tools were not motorically iconic signs, e.g., fingerspelling "chopsticks," instead of producing the motorically iconic sign CHOPSTICKS. Thus, subjects were both accurate and produced the expected form-types within each naming condition.

Statistically significant activity can be seen in Fig. 3 and in Table 1 (critical t value for the whole brain volume is ± 4.70). The contrast between naming actions with handling classifier verbs and the control task demonstrated activation of left posterior middle temporal gyrus, and as predicted, left premotor cortex (-39, -1, +41) and left inferior parietal cortex, BA 40 (-54, -35, +30), although with minimal clusters. The contrast between naming tools and the control task demonstrated activation in left premotor and inferior parietal cortex, with similar activation maxima (L premotor: -40, 0, +35; L IPL: -55, -31, +33), but with larger clusters of activation. Activation was also observed in left posterior inferior temporal (IT) cortex for naming tools (-50, -51, -10), but not in posterior middle temporal cortex. Subtraction of the control task from naming actions performed without an implement revealed activation in left posterior middle temporal gyrus but no activation in left premotor or left IPL.

In addition, contrasts between each naming task and the control task showed activation in left inferior frontal gyrus, with nearly identical maxima co-ordinates (see Table 1 and Fig. 3). Left IFG activation was predicted for handling classifier verbs if their production involved phonological encoding, rather than pantomimic articulation. Although both tool naming and action naming with handling classifier verbs resulted in activation in the superior parietal lobule, naming actions performed *without* a tool also resulted in activation in SPL. The activation maxima in SPL were nearly identical for all sign types (see Table 1).



Fig. 3. Illustration of the contrasts between the three naming tasks and the control task. (A) Naming tools minus control task. (B) Naming actions performed with a tool (handling classifier verbs) minus control task. (C) Naming actions performed without a tool (general verbs) minus control task.

The contrast between naming actions performed with a tool (handling classifier verbs) and naming actions performed without an implement (general verbs) revealed no significant differences in activation. To probe the level of confidence we could place in this negative result, and specifically to address whether there may have been a small effect of verb type, but low in magnitude and therefore subthreshold, we conducted a conjunction analysis (Price & Friston, 1997). This analysis located voxels where there was a significant main effect of retrieving verbs (at a corrected level of significance, |t[65]| = 4.70), and no difference between verb types (at uncorrected significance level, |t[65]| = 1.67). The latter threshold excluded any voxels in which there was more than an approximately 1%change in activity. The conjunction analysis identified regions of equal activation for both verb types in the following regions: left IT (-46, -53, -1), left IFG (-47, +13, +6), right posterior middle temporal cortex at the junction of occipital lobe and angular gyrus

(+42, -72, +19), left premotor (-39, -1, +42), and left IPL (-54, -36, +5). Importantly, the conjunction analysis revealed no significant differences between these verb types, even at the uncorrected level of significance.

Finally, the contrast between naming actions performed with a tool and naming tools revealed activation in posterior right middle temporal gyrus (+49, -58, +5; t=4.82), right angular gyrus (+39, -69, +18; t=4.74), and the occipital pole (+1, -86, -2; t=4.95). There was more activation in these regions when ASL signers named tool-related actions. The first two activation sites correspond to area MT in the right hemisphere.

4. Discussion

The sensory-motoric iconicity of ASL signs denoting tools (e.g., SCREWDRIVER) and of handling classifier verbs denoting actions performed with a tool (e.g., STIR) does not appear to alter the neural systems that Table 1

Region	Naming tools minus control task				Naming actions performed with a tool (handling classifier verbs) minus control task				Naming actions performed without a tool (general verbs) minus control task			
	T ₈₈ coords.			Threshold	T ₈₈ coords.			Threshold	T ₈₈ coords.			Threshold
	x	у	Ζ	<i>t</i> (dof)	x	у	Z	<i>t</i> (dof)	x	У	Z	<i>t</i> (dof)
Frontal lobe												
IFG L	-42	+28	+18	+5.73	-46	+26	+13	+5.19	-47	+21	+15	+5.23
Premotor L	-40	0	+35	+5.13	-39	-1	+41	+4.71				
Temp. lobe												
Post. MTG L					-49	-59	0	+5.64	-49	-61	+11	+5.36
Post. IT L	-50	-51	-10	+5.89								
Ventral IT L									-23	-38	-10	+5.07
R									+28	-34	-15	+4.89
Ant. IT R					+35	-10	-29	+4.83				
Parietal lobe												
IPL L	-55	-31	+33	+5.15	-54	-35	+30	+4.70				
R									+42	-71	+19	+4.88
SPL L	-31	-43	+55	+5.51	-25	-41	+55	+5.10	-22	-43	+58	+5.23
R	+27	-36	+60	+4.77	+23	-39	+65	+4.83				
Occipital lobe												
Lingual gyrus R	+4	-69	+12	+5.41	+5	-65	+6	+5.47	+4	-67	+11	+5.85
Supracalcarine L	-19	-82	+3	+4.90	-27	-84	+23	+4.88				

Maxima for action and object naming minus the control task in the whole brain analysis (critical $t \pm 4.70$)

Abbreviations. IFG, inferior frontal gyrus; MTG, middle temporal gyrus; IT, inferior temporal cortex; IPL, inferior parietal lobule; SPL, superior parietal lobule.

underlie lexical retrieval or sign production. When either English speakers or ASL signers name tools or name actions performed with a tool, very similar neural regions within left premotor and left inferior parietal cortex are engaged. The neural activation maximum observed within left premotor cortex for naming actions performed with a tool in ASL (-39, +1, +41) was similar to the premotor activation observed when English speakers named the function or use of tools (-39, -6, +51; Grafton et al., 1997). Naming tools with iconic ASL signs also engaged left premotor cortex (-40, 0, +35), and this activation maximum was similar to that found when English speakers named tools: -52, +11, +29 (Grabowski et al., 1998); $-50(\pm 6)$, $+3(\pm 4), 25(\pm 8)$ (Chao & Martin, 2000).

In addition to left premotor cortical activation, naming tools or naming actions performed with a tool engaged the left inferior parietal lobule. The activation maximum in left IPL for naming actions with ASL handling classifier verbs (-54, -35, +30) was similar to the activation maximum observed when English speakers named actions performed with an implement (-55, -27, +29; Damasio et al., 2001). Similarly, the activation maximum in left IPL observed when ASL signers retrieved iconic signs for tools (-55, -31, +33)was similar to the maximum observed when English speakers retrieved words for tools (although activation for ASL was slightly more inferior than that observed English speakers): -48, -36, +56,for and -40, -34, +44 (Okada et al., 2000); $-30(\pm 3), -39(\pm 2),$ +47(±1) (Chao & Martin, 2000).

Thus, recognizing and naming tools or tool-based actions engage a left premotor-parietal cortical network for both signers and speakers. Activation within this network may represent the retrieval of knowledge about the sensory- and motor-based attributes that define human tool-use. A third cortical area, left inferior temporal (IT) cortex (BA 37), also appears to be engaged when speakers or signers name tools from visually presented pictures. Many studies have reported activation in posterior left IT when speakers name tools, with nearly identical activation maxima to those reported (-52, -50, -10,here Damasio et al., 1996: -50, -52, -8, Okada et al., 2000). The ability to recognize and name tools or manipulable man-made objects therefore depends on the integration of information from both the ventral and dorsal streams. Crucially, the sensory-motoric form of ASL signs does not appear to alter activation within this cortical network.

As noted in the introduction, the few studies investigating the production of pantomimic gestures depicting tool use report additional activation within the left superior parietal lobule (Choi et al., 2001; Johnson et al., 2002; Moll et al., 2000). In our study, activation in left SPL was also observed, but for all sign-types, including general verbs that do not exhibit pantomimic iconicity. The fact that left SPL activation was found for ASL general verbs argues against the hypothesis that SPL activation reflects the motor-planning of actions computed according to the visuospatial characteristics of an object (Choi et al., 2001). That is, left SPL activation does not appear to reflect the planning or control of pantomimic gesture related to object use. Rather, we speculate that this activation reflects aspects of the control or monitoring of learned motor movements. For example, activation in the superior parietal lobule has been observed for writing (Katanoda, Yoshikawa, & Sugishita, 2001; Meson & Desmond, 2001) and for other over-learned finger or hand movements (Krings et al., 2000).

We found little evidence that the pantomimic iconicity of ASL handling classifier verbs has an effect on the neural systems that underlie their production. Both the conjunction analysis and the direct contrast between handling classifier verbs and ASL verbs that are not motorically iconic revealed no significant differences in neural activation. It is somewhat surprising that these analyses did not reveal more activation within left premotor-parietal cortices for the handling classifier verbs relative to general verbs, based on the semantics of handling verbs. However, lack of activation within these cortices may be due to the fact that many of the pictures depicting actions performed without a tool, nonetheless occasionally contained a manipulable object (e.g., a book for read, a candle for blow out, a swing for swing, a ball for kick). It is possible that recognition of these objects lead to weak activation within left premotor-parietal cortices during the lexical retrieval for the general verbs. Another possibility is that left inferior parietal cortex, specifically, the supramarginal gyrus (SMG), is also engaged during the phonological implementation of ASL signs. Corina et al. (1999) found that stimulation to left SMG resulted in handshape substitutions in a picture-naming task by a deaf ASL signer. Emmorey et al. (2003) also found activation in left SMG when naming animals with ASL signs was contrasted with naming animals using fingerspelling. Fingerspelled forms have a different representation and violate many of the phonological constraints found for native signs (Brentari & Padden, 2001). Thus, left SMG may partially subserve phonological feature selection for ASL signs in general, and this additional function may account for the lack of difference in neural activation within parietal cortex between ASL handling classifier verbs and general verbs. That is, the selection of phonological features may engage inferior parietal cortex during the production of both verb types. Given the resolution of PET imaging, it may not be possible to observe additional activation within this region for naming tool-based actions (handling classifier verbs) due to the retrieval of conceptual knowledge about tool-use.

Furthermore, the finding that the production of all sign types engaged left inferior frontal gyrus (Broca's area, BA 44/45) represents additional evidence that handling classifier verbs and iconic signs for tools are lexical forms, rather than gestural pantomimes. Data from neuroimaging studies (and from lesion studies) indicate that Broca's area contributes to phonological encoding during speech production (see Indefrey & Levelt, 2000, for a review). The fact that sign language production engages Broca's area suggests that the functional specialization of this neural region is not dependent on the motor systems involved in language production. Rather, the abstract nature of phonology as a level of linguistic representation may be the primary factor that drives the organization of neural systems underlying language production.

Finally, our results are complemented by two case studies of aphasic signers who exhibit a dissociation between the ability to sign and to pantomime (Corina et al., 1992; Marshall, Atkinson, Smulovitch, Thacker, & Woll, in press). Corina et al. (1992) describe the case of WL who had a large frontotemporoparietal lesion in the left hemisphere. The lesion included Broca's area (BA 44/45), the arcuate fasciculus, a small portion of inferior parietal lobule (BA 40) and considerable damage to the white matter deep to the inferior parietal lobule. WL exhibited poor sign comprehension, and his signing was characterized by phonological and semantic errors with reduced grammatical structure. An example of a phonological error by WL was his production of the sign SCREWDRIVER. He substituted an A-bar handshape (fist with thumb extended, touching the palm of the non-dominant hand) for the required H handshape (see Fig. 1B). In contrast to his sign production, WL was unimpaired in his ability to produce pantomime. For example, instead of signing DRINK (a "C" handshape as in CUP, see Fig. 1, moves toward the mouth, with wrist rotation-as if drinking), WL cupped his hands together to form a small bowl. WL was able to produce stretches of pantomime and tended to substitute pantomimes for signs, even when pantomime required more complex movements. Such pantomimes were not evident before his brain injury.

Marshall et al. (in press) report a second case of a deaf aphasic signer who also demonstrated a striking dissociation between gesture and sign (in this case, British Sign Language). "Charles" had a left temporoparietal lesion and exhibited sign anomia that was parallel to speech anomia. For example, his sign finding difficulties were sensitive to sign frequency and to cueing, and he produced both semantic and phonological errors. However, his gesture production was intact and superior to his sign production even when the forms of the signs and gestures were similar. Furthermore, this dissociation was impervious to the iconicity of signs. His production of iconic signs was as impaired as his production of non-iconic signs. Thus, the lesion data support the neuroimaging results presented here. The neural systems supporting sign language production and pantomimic expression are non-identical.

Because signed languages are produced with the same articulators involved in grasping, reaching, and pantomiming, we raised the question of whether lexical retrieval for signs that have a high degree of sensorimotoric iconicity might engage different neural systems compared to non-iconic signs. At least within the limits of the PET paradigm, our results indicate no difference in neural activation between the retrieval of motoriconic signs and signs that do not exhibit such iconicity. Furthermore, even when the form of a sign is indistinguishable from a pantomimic gesture, the neural systems underlying its production mirror those engaged when hearing speakers produce (non-iconic) words referring to the same types of entities, i.e., tools or tool-based actions.

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