

Author's Accepted Manuscript

An fMRI study of perception and action in deaf signers

Kayoko Okada, Corianne Rogalsky, Lucinda O'Grady, Leila Hanaumi, Ursula Bellugi, David Corina, Gregory Hickok



PII: S0028-3932(16)30014-8
DOI: <http://dx.doi.org/10.1016/j.neuropsychologia.2016.01.015>
Reference: NSY5857

To appear in: *Neuropsychologia*

Received date: 19 May 2015
Revised date: 11 January 2016
Accepted date: 13 January 2016

Cite this article as: Kayoko Okada, Corianne Rogalsky, Lucinda O'Grady, Leila Hanaumi, Ursula Bellugi, David Corina and Gregory Hickok, An fMRI study of perception and action in deaf signers, *Neuropsychologia*, <http://dx.doi.org/10.1016/j.neuropsychologia.2016.01.015>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting galley proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

An fMRI Study of Perception and Action in Deaf Signers

Kayoko Okada^{1,5}, Corianne Rogalsky², Lucinda O'Grady³, Leila Hanaumi³, Ursula Bellugi³,David Corina⁴, Gregory Hickok⁵¹Department of Psychological Sciences, Whittier College, Whittier, CA²Department of Speech and Hearing Science, Arizona State University, Tempe, AZ³Laboratory for Cognitive Neuroscience, The Salk Institute for Biological Studies, San Diego, CA⁴Department of Linguistics, University of California, Davis, CA⁵Department of Cognitive Sciences, University of California, Irvine, CA

Running title: Perception and Action

Correspondence: Gregory Hickok, Department of Cognitive Sciences, University of California at Irvine, Irvine, CA 92697-3800. Phone: 949-824-1409. Fax: 949-824-2307. E-mail: greg.hickok@uci.edu

Abstract

Since the discovery of mirror neurons, there has been a great deal of interest in understanding the relationship between perception and action, and the role of the human mirror system in language comprehension and production. Two questions have dominated research. One concerns the role

of Broca's area in speech perception. The other concerns the role of the motor system more broadly in understanding action-related language. The current study investigates both of these questions in a way that bridges research on language with research on manual actions. We studied the neural basis of observing and executing American Sign Language (ASL) object and action signs. In an fMRI experiment, deaf signers produced signs depicting actions and objects as well as observed/comprehended signs of actions and objects. Different patterns of activation were found for observation and execution although with overlap in Broca's area, providing prima facie support for the claim that the motor system participates in language perception. In contrast, we found no evidence that action related signs differentially involved the motor system compared to object related signs. These findings are discussed in the context of lesion studies of sign language execution and observation. In this broader context, we conclude that the activation in Broca's area during ASL observation is not causally related to sign language understanding.

KEYWORDS: Sign Language; ASL Observation; ASL Production; Perception and Action; Broca's Area; Neuroimaging; fMRI

The relation between sensory and motor systems has become a topic of intense interest across several research areas. In work on motor control one important question is how sensory targets for action—e.g., the location, shape, size, and orientation of an object to be grasped—are transformed into motor plans and, conversely, how motor plans are used to generate sensory predictions of their consequences (Andersen, 1997; Kawato, 1999; Shadmehr & Krakauer, 2008; Wolpert, 1997). In perceptual research there has been an effort to understand whether and how motor systems might participate in perception (D'Ausilio et al., 2009; Hickok, 2014; Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007). In the conceptual knowledge domain embodied cognition approaches have asked whether motor systems play a role in action-related concepts (Boulenger, Hauk, & Pulvermuller, 2008; de Zubicaray, Arciuli, & McMahon, 2013; Gallese &

Lakoff, 2005; Grossman et al., 2008; Hauk, Johnsrude, & Pulvermuller, 2004; Hickok, 2015; Kemmerer, 2015).

The discovery of mirror neurons in the macaque premotor cortex has helped fuel this interest, particularly with respect to the role of motor systems in perception and in conceptual knowledge representation. Mirror neurons are cells that fire in response to performing an action as well as to observing the same or similar action and they have been argued to form the “basis” of action understanding (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Craighero, 2004) as well as a host of other functions including empathy (Gallese, 2001), autism (Gallese, 2006; Williams, Whiten, Suddendorf, & Perrett, 2001), and language (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004). With respect to language, the topic of the present investigation, mirror neurons generated excitement about three hypotheses. One was that receptive speech functions rely on motor circuits located within the human mirror system (Gallese et al., 1996), precisely in the manner suggested by Liberman's motor theory of speech perception (Galantucci, Fowler, & Turvey, 2006; Liberman & Mattingly, 1985). The second was that motor networks play a critical role in the representation of conceptual knowledge of actions (Pulvermuller, 2005; Pulvermuller & Fadiga, 2010). And the third was that the proposed action understanding function of monkey mirror neurons provided a precursor to the evolution of language in humans (Rizzolatti & Arbib, 1998), suggesting a manual gesture origin (Corballis, 2010).

The vast majority of research aimed at assessing these hypotheses, the first two in particular, has focused on spoken language, leading to much debate. On one hand, there is ample evidence that the motor system activates during speech perception (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Wilson, Saygin, Sereno,

& Iacoboni, 2004) and that disruption of motor function can, in some cases, result in changes in performance on some tasks (D'Ausilio et al., 2009; Grossman et al., 2008; Meister et al., 2007; Mottonen & Watkins, 2009; Schomers, Kirilina, Weigand, Bajbouj, & Pulvermuller, 2014; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). On the other hand, there is compelling evidence that the basic ability to perceive and understand speech is not substantially affected by chronic damage to motor speech systems (Hickok, Costanzo, Capasso, & Miceli, 2011; Rogalsky, Love, Driscoll, Anderson, & Hickok, 2011), acute and complete deactivation of motor speech ability (Hickok et al., 2008), or the failure to develop articulate speech (Bishop, Brown, & Robson, 1990).

Signed languages, being largely manual-based language systems, provide an interesting arena for the investigation of these issues because they provide a bridge between sensorimotor processes in language and manual gesture. Signed languages are natural language systems that have emerged spontaneously in Deaf communities throughout the world (Emmorey, 2002; Klima & Bellugi, 1979). Like spoken languages, they exhibit a hierarchical organization at multiple levels including syntactic, morphological, and phonological structure (Emmorey, 2002). Research on the neural basis of signed language has revealed a similar pattern of hemispheric asymmetries (Corina, 1998; Hickok, Bellugi, & Klima, 1998a, 1998b; Poizner, Klima, & Bellugi, 1987), similar aphasic deficits following brain injury (Hickok & Bellugi, 2001), and, relevant to the present work, the involvement of classic language regions including Broca's area (Corina et al., 1999; Hickok, Kritchvsky, Bellugi, & Klima, 1996; Neville et al., 1998). In functional imaging research on signed languages, Broca's area has been found to be activated during the imagined or overt signing of sentences (Braun, Guillemin, Hosey, & Varga, 2001;

Horwitz et al., 2003; McGuire et al., 1997; Sakai, Tatsuno, Suzuki, Kimura, & Ichida, 2005), words (Emmorey et al., 2004) and non-sense signs (Buchsbaum et al., 2005; Pa, Wilson, Pickell, Bellugi, & Hickok, 2008) and Broca's area has also been found to activate during the observation of signed language (Buchsbaum et al., 2005; MacSweeney et al., 2004; MacSweeney et al., 2002; Neville et al., 1998; Pa et al., 2008; Petitto et al., 2000).

These findings are consistent with the existence of a sensorimotor system for sign language and more specifically with the hypothesis that Broca's area is an important hub in this network not only for spoken language but also for signed language. However, previous experiments have not measured activation patterns during the production and observation of meaningful signs *within* subjects, rendering the evidence for a shared sensorimotor network circumstantial. One aim of the present study was to fill this gap in the literature by using fMRI to measure the neural response to both observation and generation of signs in the same groups of participants. Regions of overlap between sign observation and production will identify the sensorimotor network for sign processing and test the hypothesis that Broca's area is part of that network.

Another aim of the present study was to investigate the possibility that action versus object sign production and/or comprehension would differentially activate motor areas (action > object signs), as embodied language models predict (Hauk, Davis, Kherif, & Pulvermuller, 2008; Moseley & Pulvermuller, 2014; Pulvermuller, Shtyrov, & Ilmoniemi, 2005). A previous study of sign language production reported greater activation in motor-related areas (premotor cortex, Broca's region, pre-SMA) during the generation of verb signs related to presented noun signs (i.e., a verb generation task) compared to repetition of noun signs (San Jose-Robertson, Corina,

Ackerman, Guillemin, & Braun, 2004). This would seem to support embodied cognition claims of more motor involvement for action-related signs. However, the noun and verb tasks were not equated for difficulty and complicate this conclusion. In the present study we used both a naming and a comprehension matching task for both the action- and object-related conditions and in fact used the same base visual stimulus (an object-oriented action video clip) in both object- and action-related conditions. This provided a much tighter match in terms of the task and stimuli, which allowed us to assess the effects specific to processing object versus action signs.

The present fMRI study sought to assess two hypotheses:

Hypothesis 1: Broca's area serves a sensorimotor function for sign language. This hypothesis predicts that we will observe activation overlap in Broca's area for sign observation and production within subjects. Observation-production overlap in other areas, such as posterior parietal regions, is also expected and the overall pattern of overlap will serve to delineate the sensorimotor network for sign. Of course, because fMRI is a correlational measure, the outcome of our study cannot directly address the *function* of the sensorimotor network, for example, whether or not it supports sign understanding as the mirror neuron theory of action understanding holds. This question is taken up in the discussion.

Hypothesis 2: Motor-related areas will respond more strongly during the processing of action signs compared to object signs. Because such effects have been reported in a number of motor-related regions, including primary motor cortex, premotor cortex, and Broca's area (for review see Aziz-Zadeh & Damasio, 2008), we did not have a specific prediction regarding where in the

motor system we might find such an effect. Again, should this hypothesis be confirmed, it will not provide direct evidence for the causal involvement of motor systems in action semantics, however, failure to observe a difference would represent a non-replication of previously reported effects in spoken language.

To assess these hypotheses, on each trial native Deaf signers viewed a video clip of an action involving an object (e.g., swinging a tennis racquet) and then in different conditions, (1) generated a sign naming the action, (2) generated a sign naming the object, (3) viewed a sign that named the action, or (4) viewed a sign that named the object. To preview our major findings, we report that viewing versus generating signs yielded robust differences in expected regions (visual versus motor), that common areas of activation for the sign observation and production conditions included Broca's area, and that action-related signs did not yield more activation in motor-related regions.

Methods

Subjects

The study was approved by the Institutional Review Boards of University of California, Irvine, and the Salk Institute for Biological Studies. Sixteen participants (11 females) between 18 and 45 years of age were recruited by researchers at the Salk Institute for Biological Studies and were scanned at the Research Imaging Center at UC Irvine. Participants received monetary compensation for their time. The volunteers were right-handed, native deaf signers of American Sign Language (ASL) with normal or corrected-to-normal vision, no known history of neurological disease, and no other contraindications for MRI as reported on the metal screening questionnaire. All volunteers were exposed to ASL from birth and were born to deaf parents.

Fifteen of the sixteen subjects were deaf at birth and one subject became deaf at 2.5 years of age. All participants had completed high school, seven had completed a bachelor's degree or higher, and three participants were attending college at the time the study was conducted. All were proficient with written English. Handedness was self reported on a background questionnaire and was also measured using the Edinburgh Handedness Inventory. Written informed consent was obtained from each participant prior to participation in the study. One subject (male, age=27) was omitted from data analysis for failing to remain on task during the experiment (Total N=15, Female=11, Male=4).

Stimuli & Task

FMRI was used to monitor BOLD changes elicited while participants viewed video clips depicting an action with an object (e.g. swinging a tennis racket), and participants either generated the name of the action or object, or made a match/no-match judgment between the action/object and a subsequently signed name of an action or object. The experiment was a factorial block design crossing Sign Type (Object or Action) x Task Type (Matching/Observe or Naming/Execute). Each 20-second block started with instructions on screen for 1.5 s to either "name the object", "name the action", "match the object" or "match the action". Following the instructions, a white fixation appeared on screen for 500 ms, and then participants were presented with an 18 s sequence of videos and they either generated a sign for the action or object, or matched the action or object. Naming (or "generate") blocks were created by concatenating 3 video clips together. Each video clip was 2 s in length which was followed by a white fixation that remained on screen for 4 s interval during which time participants generated the sign for the object or action. Participants generated the appropriate sign for the action or the

object using their right hand. Three such video events were concatenated together to create an 18 s block. This was followed by a 10 second rest interval during which time a white fixation remained on screen until instructions for the next block appeared on screen.

For the matching task, blocks were also 20 seconds in length. The blocks started with 1.5 s of instructions followed by a white fixation that remained on screen for 500ms. This was followed by a sequence of pairs of videos. After the first video clip (~2 s), a second video clip showing the sign for the object or action was presented (~2 s), which was followed by a white fixation that remained on screen for 2 s. When the white fixation appeared on screen, participants indicated with a button press whether or not the 2nd video clip semantically matched the first video clip (e.g. video of swinging a tennis racket, followed by a video of a person signing basketball is a mismatch). Participants pressed a button with their non-dominant hand (left hand since subjects were right handed) if the videos were not semantically congruent. Three such video-pair events were concatenated together to create an 18 s video block. Like the naming blocks, this was followed by a 10s rest interval during which time subjects fixated on a white plus sign. Two blocks in each session contained non-matching signs and these blocks were eliminated from data analysis. Figure 1 illustrates the timing and structure of the naming and matching blocks in the experiment.

The experiment consisted of four sessions (or runs) and each session consisted of two blocks of each experimental type each experimental condition (e.g. match action, match object, name action, or name object, “non-matching”), totaling 10 blocks per session. A total of 24 video clips were used in the experiment and each video clip was ~2 sec in length. The stimuli used in the study are listed in the Appendix. The 24 videos were repeated 5 times throughout the

experiment (for a total of 120 trials) and the order of presentation was randomized across trials and across participants. Randomization was achieved by assigning each set of the 24 videos to a condition (e.g. Set1= “name the action”, Set2=“name the object”, Set3=“match the action”, Set4=“match the object” and Set5=“non-matching/toss”) and then permuting the order of the videos. After permutation, videos were sequentially grouped into sets of three. Another random permutation was performed in Matlab to determine the order of the conditions for each session for each subject.

The study started with a short practice session consisting of 1 block of stimuli from each experimental condition to familiarize subjects with the task. Subjects were scanned during the practice session to acclimatize them to the fMRI environment. Videos used in the practice session were not used in the experiment. The study ended with a high resolution structural scan and the entire experiment was 1 hour in length. Stimuli presentation and timing was controlled using Cogent software (http://www.vislab.ucl.ac.uk/cogent_2000.php) implemented in Matlab 7.1 (Mathworks, Inc, USA) running on a dual-core IBM Thinkpad laptop.

Imaging

MR images were obtained in a Philips Achieva 3T (Philips Medical Systems, Andover, MA) fitted with an 8 channel RF receiver head coil, at the Research Imaging Center scanning facility at the University of California, Irvine. Images during the experimental sessions were collected using Fast Echo EPI (sense reduction factor=1.5, matrix=112x112mm, TR=2.0s, flip angle = 70°, TE=30 ms, size=1.95x1.95x2.5 mm). A total of 560 echo planar images (EPI) were collected over 4 sessions, and 37 slices provided whole brain coverage. After the functional scans, a high resolution T1-weighted anatomical image was acquired with an MPRAGE pulse

sequence in axial plane (matrix=256x256mm, TR=8 ms, TE=3.6 ms, flip angle=8°, size=1x1x1 mm).

Data Analysis

Data preprocessing and analyses were performed using AFNI software (Cox, 1996). First, motion correction was performed by creating a mean image from all of the volumes in the experiment and then realigning all volumes to that mean image using a 6-parameter rigid-body model (Cox & Jesmanowicz, 1999). The images were high pass filtered at 0.008 Hz and spatially smoothed with an isotropic 6 mm full width half maximum (FWHM) Gaussian kernel. The anatomical image for each subject was coregistered to his/her mean EPI image. First level analysis was performed on the time course of each voxel's BOLD response for each subject using AFNI software (Cox, 1996). Analysis was performed using AFNI's 3dDeconvolve function and regressors for each of the five conditions were created by convolving the gamma variate function with a square wave of duration 18 s to model the experimental blocks. A total of 11 regressors were entered into a General Linear Model: Four regressors representing each experimental condition (match object, match action, name object, name action), 1 to model "non-match" trials, and 6 motion regressors. Parameter estimates for the events of interest were obtained and statistical maps were created. To facilitate group level analysis, the statistical maps for each participant were transformed into standardized space (Talairach & Tournoux, 1988) using a Talairach template and resampled into 2mm³ voxels. Group analysis included 15 of the 16 participants and one participant was eliminated for failing to following instructions. Data were analyzed using a 2 (Sign Type: Action vs. Objects) x 2 (Task Type: Naming vs. Matching) analysis of variance (ANOVA) using AFNI's 3dANOVA3 function and parameter

estimates from each participant were entered into a random effects model. An F-test was calculated to test the main effect of sign type, main effect of task type, and an interaction between the two factors. T-tests were also performed to reveal the directionality of the contrasts: naming > matching, matching > naming, actions > objects and objects > actions. Group level activation maps were created and a cluster-wise significance level was calculated based on Monte Carlo simulations implemented in AFNI's 3dClustSim program (Ward, 2000) to correct for multiple comparisons and maintain a corrected $\alpha < .05$ (43 voxels at 2 mm voxel resolution, $p < .001$).

In addition, we identified regions of overlap in the naming and matching tasks. To look for group level effects, AFNI's 3dttest++ function was used to identify regions significantly activated for naming tasks (naming objects + naming actions > baseline) and separately for the matching tasks (matching objects + matching actions > baseline). Two separate masks were created (each thresholded at $p < .01$, corrected), and then a conjunction mask was created to identify regions of overlap in the matching and naming tasks. In addition to looking at group level effects, we also identified regions of overlap in each individual subject. For each subject, two masks were created: one mask to identify regions activated in naming tasks ($p < .01$), and another mask to identify regions activated in the matching tasks ($p < .01$). An overlap map was generated from these two to identify areas common to both tasks. The results of both analyses are reported below.

Results

Behavioral performance on the matching task was at 94% accuracy confirming that the subjects stayed on task. Compliance on the naming task was confirmed on each naming block

for each subject by experimenter monitoring through the console window.

Group analysis revealed a significant main effect of sign type ($p < .001$, corrected), a significant main effect of task type ($p < .001$, corrected) and no significant interaction between the two factors. A significant effect of sign type was observed in the middle frontal gyrus (MFG) in the left hemisphere (see Table 1 and Figure 2). T-tests revealed that the contrast of objects>actions yielded a large cluster of activation in left MFG but the opposite contrast did not reveal significant activations in cortex. The main effect of task type revealed several large activations, and a contrast of naming > matching yielded activations in bilateral superior temporal gyrus, cerebellum, left inferior frontal cortex, right middle frontal cortex and bilateral inferior parietal cortex, regions typically observed in language production studies. The reverse contrast of matching > naming revealed activation in bilateral STS/STG and visual cortex. Areas significantly activated in each contrast are illustrated in Figure 3 and peak Talairach coordinates for the significant clusters are outlined in Table 1.

A conjunction analysis was also performed to identify regions of overlap for naming and matching tasks (i.e. regions supporting execution and comprehension). Both group level analysis and single subject analyses were performed. As described in the methods, to create conjunction maps, we first created two statistical maps for each subject: naming tasks (naming actions + naming objects > baseline) and matching tasks (matching actions + matching objects). Two maps were created to identify regions associated with naming ($p < .01$) and separately for matching ($p < .01$), and an intersection map was created to find regions of overlap. For group level analyses, we performed two T-tests to identify regions activated in the naming tasks and also regions activated in the matching tasks. Two masks were created (each thresholded at $p <$

.01, corrected) and then a conjunction mask was created to identify regions common to both tasks at the group level (Figure 4, Table 2). We found areas of overlap in bilateral superior and middle temporal gyrus, bilateral inferior frontal cortex, parahippocampal gyrus, right supramarginal gyrus and cerebellum.

In addition to group analysis, we examined the conjunction maps in individual subjects and compared the maps to the group results. In all 15 subjects, we found that individual subjects activated the bilateral visual cortex, bilateral posterior middle temporal gyrus and the cerebellum. Thirteen of the 15 subjects activated right inferior frontal cortex, twelve activated the left inferior frontal cortex, and 10 activated inferior parietal cortex. Table 2 includes the number of subjects who showed activation in the same cluster as identified in the group map. In addition, Figure 5 illustrates overlap maps from several representative subjects.

Discussion

The present study examined the brain response during the perception and production of American Sign Language signs by a group of native Deaf signers. In terms of basic activation patterns during perception versus production, we report expected results: sign perception (matching observed object-oriented actions to signs naming the actions or objects) yielded greater activation in vision-related cortices and in the superior temporal lobe bilaterally compared to the naming task, while sign production (naming) yielded more activation in bilateral superior temporal gyrus, cerebellum, left inferior frontal cortex, right middle frontal cortex and bilateral inferior parietal cortex, consistent with what has been reported previously (see Introduction for review). These differences are consistent generally with what is known about the organization of high-level vision and manual gesture. For example, the lateral occipital temporal region is well known to comprise a portion of the ventral visual stream involved in object and body part identification (Downing, Jiang, Shuman, & Kanwisher, 2001; Grill-Spector, Kourtzi, & Kanwisher, 2001) and the superior temporal sulcus is notable for its involvement in biological motion perception (Grossman et al., 2000; Jastorff, Popivanov, Vogels, Vanduffel, & Orban, 2012), all major features of sign language perception. The involvement of Broca's area and dorsolateral (pre)motor cortex in the naming task confirms several previous observations of the involvement of these regions in sign language and speech production (see Introduction). Another prominent activation during naming compared to matching was noted in the inferior parietal lobe, the anterior SMG specifically. This likely reflects secondary somatosensory cortex activation, which is located in this region (Ruben et al., 2001). The SMG has also been implicated in phonological aspects of sign production (Corina et al., 1999). Given that

somatosensory information plays an important role of motor planning and may participate in phonological level processes (Hickok, 2012; Tremblay, Shiller, & Ostry, 2003), it is possible that the SMG activation reflects a somatosensory/phonological function for sign.

Our particular interest in this experiment was in assessing (i) whether Broca's area comprised part of a sensorimotor network for signs, i.e., whether it activated both during production and perception of signs, and (ii) whether processing action-related signs would be associated with increased activation in motor-related regions compared to processing object-related signs. We found evidence to support the view that Broca's area is indeed part of the sensorimotor network for signs: this region was significantly activated during both the sign production and perception task as assessed at the group level and in a majority of individual subjects. We did not, however, find evidence for the hypothesis that action signs rely to a greater extent on motor-related areas compared to object signs: the only difference we observed in this respect was greater activation for object signs compared to action signs (the reverse of what was predicted) in the middle frontal gyrus. In what follows we first discuss the implications of the sensorimotor findings, including the role of Broca's area, and then the failure to find increased motor involvement in processing action signs.

The sensorimotor network for sign

We identified several regions with sign-related sensorimotor response properties, that is, they were active both during sign production and sign perception. These regions included not only Broca's area (as predicted), but a large swath of visual-related regions, the cerebellum, posterior middle and superior temporal regions, the posterior parietal lobe, and prefrontal cortex.

The visual cortex activations are unsurprising given that both the naming and the perceptual matching task included visual stimulation. The same is true for the posterior superior temporal regions, which are well-known to activate during the perception of biological motion (Grossman et al., 2000; Grossman, Blake, & Kim, 2004), which was present in both the action videos and in the signs. Individual subject analyses showed that these regions were jointly activated during the production and perception in all 15 participants. More interestingly, Broca's area and the posterior parietal cortex also jointly activated not only during the production of signs but also during their perception. This was not true of all participants, but certainly held for the majority (12/15). These regions are part of the dorsal sensorimotor stream and have been claimed to be part of the human mirror system (Rizzolatti & Craighero, 2004). Thus, the present results could be interpreted as support for the view that the proposed human mirror system is involved in understanding actions, including sign language actions consistent with what has been reported for speech actions (Watkins, Strafella & Paus, 2003; Wilson et al. 2004; Wilson & Iacoboni, 2006).

However, just as there is evidence against the action understanding interpretation of the speech-related activations of the proposed human mirror system (Hickok, 2009; Hickok, 2014), recent lesion evidence from sign language argues against a similar interpretation of the present functional neuroimaging data. We recently studied a group of deaf brain damaged signers and found that damage to the dorsal sensorimotor stream is not associated with sign comprehension deficits (Rogalsky et al., 2013), arguing that functional activation overlap found in the present experiment does not reflect sign or action understanding. Instead, sign comprehension deficits were associated with temporal lobe lesions, consistent with previous work (Hickok, Love-

Geffen, & Klima, 2002).

Thus the present results reinforce previous observations regarding the surprising similarity in the frontal language networks involved in speech compared to sign processing (Buchsbaum et al., 2005; Emmorey, Mehta, & Grabowski, 2007; Neville et al., 1998; Petitto et al., 2000) and are consistent with speculations regarding shared mechanisms between speech and manual action systems (Fadiga, Craighero, & D'Ausilio, 2009). However, this overlap in observation and execution in speech and sign does not necessarily suggest that Broca's area represents action "understanding." In spoken languages, the dissociation between regions *critical* for production versus comprehension is well established: Patients with Broca's aphasia typically have very large lesions encompassing left frontal motor speech regions, yet have quite intact word-level comprehension (Damasio, 1992; Hickok, Costanzo, et al., 2011; Hillis, 2007). Therefore, although Broca's area may be important for sensorimotor function in language, perhaps with some shared resources with manual action control, it is not a critical region for language comprehension for individual words and simple sentences.

Broca's area was part of a larger dorsal stream sensorimotor network that responded both during sign production and perception, including posterior parietal, and premotor cortex (Figure 4, Table 2). A previous study of nonsense sign perception and repetition reported a similar network (Buchsbaum et al., 2005). The present study thus extends previous findings to the case of real signs and in the context of a more naturalistic naming task on the production side. The function of the dorsal stream network for sign is likely motor control, similar to its role in both speech (Hickok, Houde, & Rong, 2011) and non-speech domains (Andersen, 1997; Milner & Goodale, 1995). Evidence for dorsal stream involvement in sign motor control comes from both

indirect and direct sources. Indirect evidence comes from data already discussed: dorsal stream regions are active during both perception and production of sign, but are not implicated in sign comprehension, suggesting primarily a role in production. More direct evidence comes from case studies of Deaf signers with non-fluent aphasia for sign, who have been reported to have lesions involving frontoparietal structures (Hickok et al., 1998a; Knapp & Corina, 2010; Poizner et al., 1987), and from direct cortical stimulation of Broca's area and the inferior parietal lobe, both of which were shown to have direct effects on sign production (Corina et al., 1999).

Action Semantics and Motor Cortex

Notably, there were no regions (motor-related or otherwise) more responsive to the observation of action- versus object-related signs. These findings do not support embodied theories of language comprehension. According to the theory of embodied semantics, processing conceptual-semantic information for actions recruits the same sensorimotor regions that are involved in action execution. In support of this idea are recent neuroimaging studies demonstrating that action words related to specific body parts (e.g., "hitting" is related to hands, "lick" is related to the face and "kick" is related to the legs) engage motor regions in a somatotopic manner (Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Pulvermüller, Kherif, Hauk, Mohr, & Nimmo-Smith, 2009), and more relevant to the present manipulation, demonstrations that motor-related words and sensory-related words differentially activate distinct regions within the brain (Moseley & Pulvermüller, 2014; Vigliocco et al., 2006). We did not replicate the action- versus object-effect in deaf signers executing or observing action- versus object-related signs. We did observe a difference in the opposite direction: more activation in

the middle frontal gyrus for the object- compared to the action-sign condition. One speculative explanation for this result is that the object conditions may have induced more eye movement than the action conditions due to the fact that the objects were in motion and therefore may have induced more consistent tracking behavior across subjects compared to the action condition. Thus, the MFG activity may reflect frontal eye field activation as a result. Alternatively, this region has been implicated in working memory (Ranganath, Johnson, & D'Esposito, 2003). In any case, this finding is clearly not supportive of the embodied semantics theory.

Comments on a Possible Manual Origin for the Evolution of Language

Although not a focus of the present study there is some debate regarding the evolutionary origin of human language, specifically, whether it evolved from manual or vocal communication roots (Corballis, 2010; Pinker & Bloom, 1990). The discovery of mirror neurons in monkey area F5, thought by some to be the homologue of human Broca's area (Rizzolatti & Arbib, 1998; Rizzolatti & Craighero, 2004), provided circumstantial support for the manual origin theory (Corballis, 2010) as does more recent observations of some degree of overlap in Broca's area for manual and vocal gesture (Fadiga et al., 2009). Sign language provides relevant information in this respect because it is both a manual gesture system and a full-blown human language. The present finding of Broca's area involvement in both sensory and motor aspects of sign language processing lends further *prima facie* support for a gestural origin theory of language evolution. However, it is important to recognize that this evidence is at best circumstantial (overlap between vocal and gestural communication systems) and in no way provides information on the evolutionary source of this overlap.

Conclusions

The present study confirms co-activation of Broca's area during the execution and observation of signs by deaf native signers. This is consistent with a tight functional coupling between sensory and motor sign systems, as has been demonstrated for spoken language. Such a finding does not specify the role(s) that such a coupling supports, which could include sensory guidance of sign production (e.g., via feedback control (Hickok, 2012; G. Hickok, Houde, et al., 2011; Houde & Nagarajan, 2011)) or motor involvement in sign perception (Arbib, 2004; Kilner, Friston, & Frith, 2007; Rizzolatti & Craighero, 2004). Data from lesion studies of deaf signers can adjudicate between these possibilities. These data show that damage to frontal motor systems produce sign language production deficits but not necessarily sign language comprehension deficits (Corina, 1998; Corina & Knapp, 2006; Hickok, Klima, & Bellugi, 1996; Poizner et al., 1987), similar to what is found in hearing/speaking individuals (Hickok, 2014).

References

- Andersen, R. (1997). Multimodal integration for the representation of space in the posterior parietal cortex. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 352, 1421-1428.
- Arbib, M. A. (2004). *Beyond the mirror*. Oxford: Oxford University Press.
- Aziz-Zadeh, L., & Damasio, A. (2008). Embodied semantics for actions: findings from functional brain imaging. *J Physiol Paris*, 102(1-3), 35-39. doi:10.1016/j.jphysparis.2008.03.012
- Bishop, D. V., Brown, B. B., & Robson, J. (1990). The relationship between phoneme discrimination, speech production, and language comprehension in cerebral-palsied individuals. *J Speech Hear Res*, 33(2), 210-219.
- Boulenger, V., Hauk, O., & Pulvermuller, F. (2008). Grasping Ideas with the Motor System: Semantic Somatotopy in Idiom Comprehension. *Cereb Cortex*.
- Braun, A. R., Guillemin, A., Hosey, L., & Varga, M. (2001). The neural organization of discourse: an H2 15O-PET study of narrative production in English and American sign language. *Brain*, 124(Pt 10), 2028-2044.
- Buchsbaum, B., Pickell, B., Love, T., Hatrak, M., Bellugi, U., & Hickok, G. (2005). Neural substrates for verbal working memory in deaf signers: fMRI study and lesion case report. *Brain Lang*, 95(2), 265-272.
- Corballis, M. C. (2010). Mirror neurons and the evolution of language. *Brain and Language*, 112(1), 25-35. doi:10.1016/j.bandl.2009.02.002
- Corina, D. (1998). The processing of sign language: Evidence from aphasia *Handbook of neurolinguistics* (pp. 313-329). San Diego: Academic Press.
- Corina, D. P., & Knapp, H. (2006). Sign language processing and the mirror neuron system. *Cortex*, 42(4), 529-539.
- Corina, D. P., McBurney, S. L., Dodrill, C., Hinshaw, K., Brinkley, J., & Ojemann, G. (1999). Functional roles of Broca's area and SMG: evidence from cortical stimulation mapping in a deaf signer. *Neuroimage*, 10(5), 570-581.
- Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, 29(3), 162-173. doi:DOI 10.1006/cbmr.1996.0014
- Cox, R. W., & Jesmanowicz, A. (1999). Real-time 3D image registration for functional MRI. *Magnetic Resonance in Medicine*, 42(6), 1014-1018. doi:Doi 10.1002/(Sici)1522-2594(199912)42:6<1014::Aid-Mrm4>3.0.Co;2-F
- D'Ausilio, A., Pulvermuller, F., Salmas, P., Bufalari, I., Begliomini, C., & Fadiga, L. (2009). The motor somatotopy of speech perception. *Current Biology*, 19(5), 381-385. doi:S0960-9822(09)00556-9 [pii]10.1016/j.cub.2009.01.017
- Damasio, A. R. (1992). Aphasia. *New England Journal of Medicine*, 326, 531-539.
- de Zubicaray, G., Arciuli, J., & McMahon, K. (2013). Putting an "End" to the Motor Cortex Representations of Action Words. *J Cogn Neurosci*. doi:10.1162/jocn_a_00437
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293(5539), 2470-2473. doi:10.1126/science.1063414

- Emmorey, K. (2002). *Language, cognition, and the brain: Insights from sign language research*. Mahwah, NJ: Lawrence Erlbaum and Associates.
- Emmorey, K., Grabowski, T., McCullough, S., Damasio, H., Ponto, L., Hichwa, R., & Bellugi, U. (2004). Motor-iconicity of sign language does not alter the neural systems underlying tool and action naming. *Brain Lang*, 89(1), 27-37.
- Emmorey, K., Mehta, S., & Grabowski, T. J. (2007). The neural correlates of sign versus word production. *Neuroimage*, 36, 202-208.
- Fadiga, L., Craighero, L., Buccino, G., & Rizzolatti, G. (2002). Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *Eur J Neurosci*, 15(2), 399-402.
- Fadiga, L., Craighero, L., & D'Ausilio, A. (2009). Broca's area in language, action, and music. *Ann N Y Acad Sci*, 1169, 448-458. doi:10.1111/j.1749-6632.2009.04582.x
- Galantucci, B., Fowler, C. A., & Turvey, M. T. (2006). The motor theory of speech perception reviewed. *Psychon Bull Rev*, 13(3), 361-377.
- Gallese, V. (2001). The 'shared manifold' hypothesis: From mirror neurons to empathy. *Journal of Consciousness Studies*, 8, 33-50.
- Gallese, V. (2006). Intentional attunement: a neurophysiological perspective on social cognition and its disruption in autism. *Brain Res*, 1079(1), 15-24.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119 (Pt 2), 593-609.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cogn Neuropsychol*, 22, 455-479.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Res*, 41(10-11), 1409-1422.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, 12, 711-720.
- Grossman, E. D., Blake, R., & Kim, C. Y. (2004). Learning to see biological motion: brain activity parallels behavior. *J Cogn Neurosci*, 16(9), 1669-1679. doi:10.1162/0898929042568569
- Grossman, M., Anderson, C., Khan, A., Avants, B., Elman, L., & McCluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*, 71(18), 1396-1401. doi:10.1212/01.wnl.0000319701.50168.8c
- Hauk, O., Davis, M. H., Kherif, F., & Pulvermuller, F. (2008). Imagery or meaning? Evidence for a semantic origin of category-specific brain activity in metabolic imaging. *Eur J Neurosci*, 27(7), 1856-1866.
- Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301-307.
- Hickok, G. (2009). Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans. *Journal of Cognitive Neuroscience*, 21(7), 1229-1243. doi:10.1162/jocn.2009.21189
- Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience*, 13(2), 135-145. doi:10.1038/nrn3158
- Hickok, G. (2014). *The myth of mirror neurons: the real neuroscience of communication and*

- cognition*. New York, NY: W.W. Norton & Company.
- Hickok, G. (2015). The Motor System's Contribution to Perception and Understanding Actions: Clarifying Mirror Neuron Myths and Misunderstandings *Language and Cognition*.
- Hickok, G., & Bellugi, U. (2001). The signs of aphasia. In R. S. Berndt (Ed.), *Handbook of neuropsychology, 2nd Edition* (Vol. 3, pp. 31-50). New York: Elsevier.
- Hickok, G., Bellugi, U., & Klima, E. S. (1998a). The neural organization of language: Evidence from sign language aphasia. *Trends Cogn Sci*, 2, 129-136.
- Hickok, G., Bellugi, U., & Klima, E. S. (1998b). What's right about the neural organization of sign language? A perspective on recent neuroimaging results. *Trends in Cognitive Science*, 2, 465-468.
- Hickok, G., Buchsbaum, B., Humphries, C., & Muftuler, T. (2003). Auditory-motor interaction revealed by fMRI: Speech, music, and working memory in area Spt. *Journal of Cognitive Neuroscience*, 15, 673-682.
- Hickok, G., Costanzo, M., Capasso, R., & Miceli, G. (2011). The role of Broca's area in speech perception: Evidence from aphasia revisited. *Brain and Language*, 119(3), 214-220. doi:10.1016/j.bandl.2011.08.001
- Hickok, G., Houde, J., & Rong, F. (2011). Sensorimotor integration in speech processing: computational basis and neural organization. *Neuron*, 69(3), 407-422.
- Hickok, G., Klima, E. S., & Bellugi, U. (1996). The neurobiology of signed language and its implications for the neural basis of language. *Nature*, 381, 699-702.
- Hickok, G., Kritchevsky, M., Bellugi, U., & Klima, E. S. (1996). The role of the left frontal operculum in sign language aphasia. *Neurocase*, 2, 373-380.
- Hickok, G., Love-Geffen, T., & Klima, E. S. (2002). Role of the left hemisphere in sign language comprehension. *Brain and Language*, 82, 167-178.
- Hickok, G., Okada, K., Barr, W., Pa, J., Rogalsky, C., Donnelly, K., . . . Grant, A. (2008). Bilateral capacity for speech sound processing in auditory comprehension: evidence from Wada procedures. *Brain and Language*, 107(3), 179-184.
- Hillis, A. E. (2007). Aphasia: progress in the last quarter of a century. *Neurology*, 69(2), 200-213.
- Horwitz, B., Amunts, K., Bhattacharyya, R., Patkin, D., Jeffries, K., Zilles, K., & Braun, A. R. (2003). Activation of Broca's area during the production of spoken and signed language: a combined cytoarchitectonic mapping and PET analysis. *Neuropsychologia*, 41(14), 1868-1876.
- Houde, J. F., & Nagarajan, S. S. (2011). Speech production as state feedback control. *Frontiers in Human Neuroscience*, 5. doi:10.3389/fnhum.2011.00082
- Jastorff, J., Popivanov, I. D., Vogels, R., Vanduffel, W., & Orban, G. A. (2012). Integration of shape and motion cues in biological motion processing in the monkey STS. *Neuroimage*, 60(2), 911-921. doi:10.1016/j.neuroimage.2011.12.087
- Kawato, M. (1999). Internal models for motor control and trajectory planning. *Curr Opin Neurobiol*, 9(6), 718-727.
- Kemmerer, D. (2015). Does the motor system contribute to the perception and understanding of actions? Reflections on Gregory Hickok's The myth of mirror neurons: the real neuroscience of communication and cognition. *Language and Cognition*. doi:<http://dx.doi.org/10.1017/langcog.2014.36>

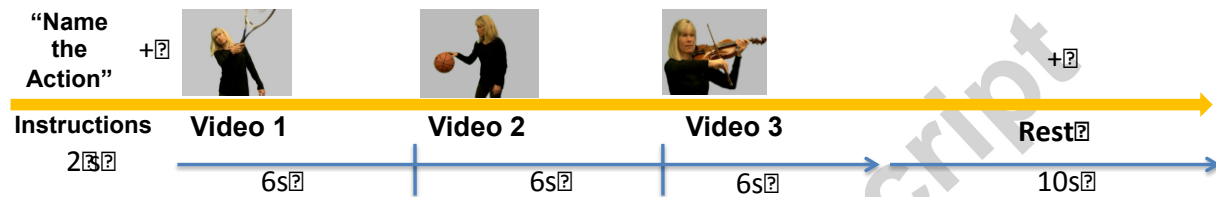
- Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., & Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: Evidence from fMRI. *Brain and Language*, 107(1), 16-43. doi:<http://dx.doi.org/10.1016/j.bandl.2007.09.003>
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007). Predictive coding: an account of the mirror neuron system. *Cogn Process*, 8(3), 159-166. doi:10.1007/s10339-007-0170-2
- Klima, E., & Bellugi, U. (1979). *The Signs of Language*. Cambridge, MA: Harvard University Press.
- Knapp, H. P., & Corina, D. P. (2010). A human mirror neuron system for language: Perspectives from signed languages of the deaf. *Brain Lang*, 112(1), 36-43. doi:10.1016/j.bandl.2009.04.002
- Lieberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition*, 21, 1-36.
- MacSweeney, M., Campbell, R., Woll, B., Giampietro, V., David, A. S., McGuire, P. K., . . . Brammer, M. J. (2004). Dissociating linguistic and nonlinguistic gestural communication in the brain. *Neuroimage*, 22(4), 1605-1618.
- MacSweeney, M., Woll, B., Campbell, R., McGuire, P. K., David, A. S., Williams, S. C., . . . Brammer, M. J. (2002). Neural systems underlying British Sign Language and audio-visual English processing in native users. *Brain*, 125(Pt 7), 1583-1593.
- McGuire, P. K., Robertson, D., Thacker, A., David, A. S., Kitson, N., Frackowiak, R. S., & Frith, C. D. (1997). Neural correlates of thinking in sign language. *Neuroreport*, 8, 695-698.
- Meister, I. G., Wilson, S. M., Deblieck, C., Wu, A. D., & Iacoboni, M. (2007). The essential role of premotor cortex in speech perception. *Current Biology*, 17(19), 1692-1696.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Moseley, R. L., & Pulvermuller, F. (2014). Nouns, verbs, objects, actions, and abstractions: local fMRI activity indexes semantics, not lexical categories. *Brain Lang*, 132, 28-42. doi:10.1016/j.bandl.2014.03.001
- Mottronen, R., & Watkins, K. E. (2009). Motor representations of articulators contribute to categorical perception of speech sounds. *Journal of Neuroscience*, 29(31), 9819-9825. 10.1523/JNEUROSCI.6018-08.2009
- Neville, H., Bavelier, D., Corina, D., Rauschecker, J., Karni, A., Lalwani, A., . . . Turner, R. (1998). Cerebral organization for language in deaf and hearing subjects: Biological constraints and effects of experience. *Proceedings of the National Academy of Sciences*, 95, 922-929.
- Pa, J., Wilson, S. M., Pickell, B., Bellugi, U., & Hickok, G. (2008). Neural organization of linguistic short-term memory is sensory modality-dependent: Evidence from signed and spoken language. *Journal of Cognitive Neuroscience*, 20, 2198-2210.
- Petitto, L. A., Zatorre, R. J., Gauna, K., Nikelski, E. J., Dostie, D., & Evans, A. C. (2000). Speech-like cerebral activity in profoundly deaf people processing signed languages: implications for the neural basis of human language. *Proc Natl Acad Sci U S A*, 97(25), 13961-13966.
- Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioral and Brain Sciences*, 13, 707-784.
- Poizner, H., Klima, E. S., & Bellugi, U. (1987). *What the hands reveal about the brain*.

- Cambridge, MA: MIT Press.
- Pulvermuller, F. (2005). Brain mechanisms linking language and action. *Nat Rev Neurosci*, 6(7), 576-582.
- Pulvermuller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nat Rev Neurosci*, 11(5), 351-360. doi:10.1038/nrn2811
- Pulvermüller, F., Kherif, F., Hauk, O., Mohr, B., & Nimmo-Smith, I. (2009). Distributed cell assemblies for general lexical and category-specific semantic processing as revealed by fMRI cluster analysis. *Human Brain Mapping*, 30(12), 3837-3850. doi:10.1002/hbm.20811
- Pulvermuller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *J Cogn Neurosci*, 17(6), 884-892.
- Ranganath, C., Johnson, M. K., & D'Esposito, M. (2003). Prefrontal activity associated with working memory and episodic long-term memory. *Neuropsychologia*, 41(3), 378-389.
- Rizzolatti, G., & Arbib, M. (1998). Language within our grasp. *Trends Neurosci*, 21, 188-194.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci*, 27, 169-192.
- Rogalsky, C., Love, T., Driscoll, D., Anderson, S. W., & Hickok, G. (2011). Are mirror neurons the basis of speech perception? Evidence from five cases with damage to the purported human mirror system. *Neurocase*, 17(2), 178-187.
- Rogalsky, C., Raphel, K., Tomkovicz, V., O'Grady, L., Damasio, H., Bellugi, U., & Hickok, G. (2013). Neural Basis of Action Understanding: Evidence from Sign Language Aphasia. *Aphasiology*, 27(9), 1147-1158. doi:10.1080/02687038.2013.812779
- Ruben, J., Schwiemann, J., Deuchert, M., Meyer, R., Krause, T., Curio, G., . . . Villringer, A. (2001). Somatotopic organization of human secondary somatosensory cortex. *Cereb Cortex*, 11(5), 463-473.
- Sakai, K. L., Tatsuno, Y., Suzuki, K., Kimura, H., & Ichida, Y. (2005). Sign and speech: amodal commonality in left hemisphere dominance for comprehension of sentences. *Brain*, 128(Pt 6), 1407-1417. doi:10.1093/brain/awh465
- San Jose-Robertson, L., Corina, D. P., Ackerman, D., Guillemin, A., & Braun, A. R. (2004). Neural systems for sign language production: mechanisms supporting lexical selection, phonological encoding, and articulation. *Hum Brain Mapp*, 23(3), 156-167.
- Schomers, M. R., Kirilina, E., Weigand, A., Bajbouj, M., & Pulvermuller, F. (2014). Causal Influence of Articulatory Motor Cortex on Comprehending Single Spoken Words: TMS Evidence. *Cereb Cortex*. doi:10.1093/cercor/bhu274
- Shadmehr, R., & Krakauer, J. W. (2008). A computational neuroanatomy for motor control. *Exp Brain Res*, 185(3), 359-381. doi:10.1007/s00221-008-1280-5
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain. 3-Dimensional proportional system: an approach to cerebral imaging*: Thieme.
- Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H., & Damasio, A. R. (2003). Neural correlates of conceptual knowledge for actions. *Cognitive Neuropsychology*, 20, 409-432.
- Tremblay, S., Shiller, D. M., & Ostry, D. J. (2003). Somatosensory basis of speech production. *Nature*, 423(6942), 866-869. doi:10.1038/nature01710
- Vigliocco, G., Warren, J., Siri, S., Arciuli, J., Scott, S., & Wise, R. (2006). The role of semantics and grammatical class in the neural representation of words. *Cereb Cortex*, 16(12), 1790-

1796. doi:10.1093/cercor/bhj115
- Ward, B. D. (2000). Simultaneous inference for fMRI data.
- Williams, J. H., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neurosci Biobehav Rev*, 25(4), 287-295.
- Wilson, S. M., Saygin, A. P., Sereno, M. I., & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nat Neurosci*, 7, 701-702.
- Wolpert, D. M. (1997). Computational approaches to motor control. *Trends Cogn Sci*, 1(6), 209-216. doi:10.1016/S1364-6613(97)01070-X

Figure 1. Structure of a single block. Both naming and matching blocks started with 2 seconds of instructions, followed by 18 seconds of videos, followed by a 10 second rest interval.

Name/Generate Condition



Match Condition



Figure 2. Main Effect of Sign Type. To determine the directionality of the effect, we performed a contrast of objects > actions, which greater activation in the left middle frontal gyrus associated with naming and matching objects compared to naming and matching actions (e.g. generating “basketball” instead of “dribble”).

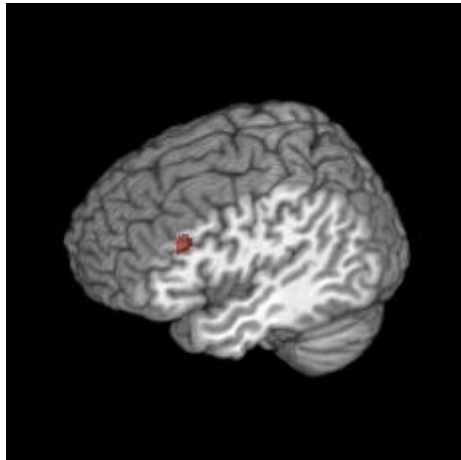


Figure 3. A contrast of naming (naming actions + naming objects) > matching (matching actions + matching objects) revealed greater activation in left IFG, Insula, motor cortex, bilateral parietal cortex. Regions in blue illustrate the reverse contrast: regions more activated during matching compared with naming.

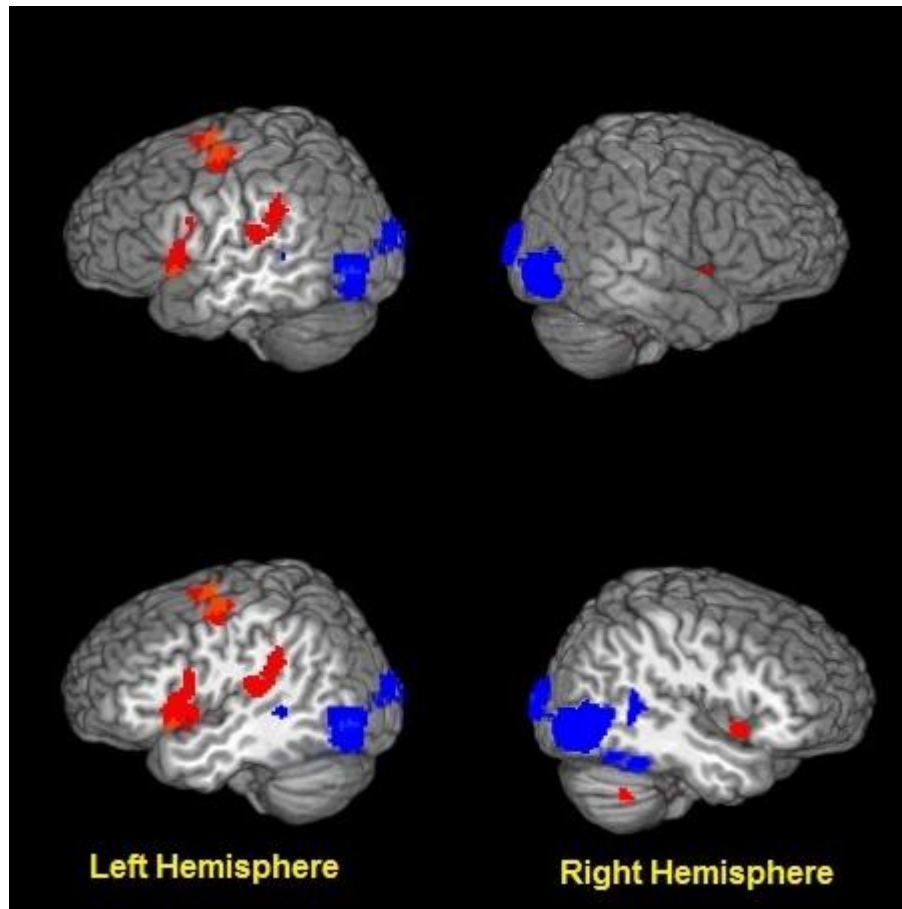


Figure 4. Group overlap map illustrating regions activated in the naming and matching tasks. Regions of overlap (ORANGE) were found in bilateral pSTG, MTG, and bilateral inferior frontal cortex.

-  **Green: Matching > Baseline**
-  **Yellow: Naming > Baseline**
-  **Orange: Overlap (Matching \wedge Naming)**

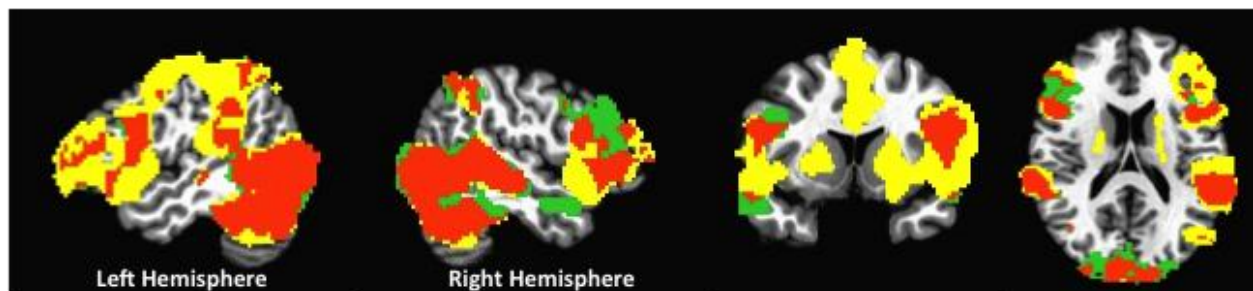


Figure 5. Individual conjunction maps for two representative subjects. These maps illustrate regions common to both naming and matching in single subjects.

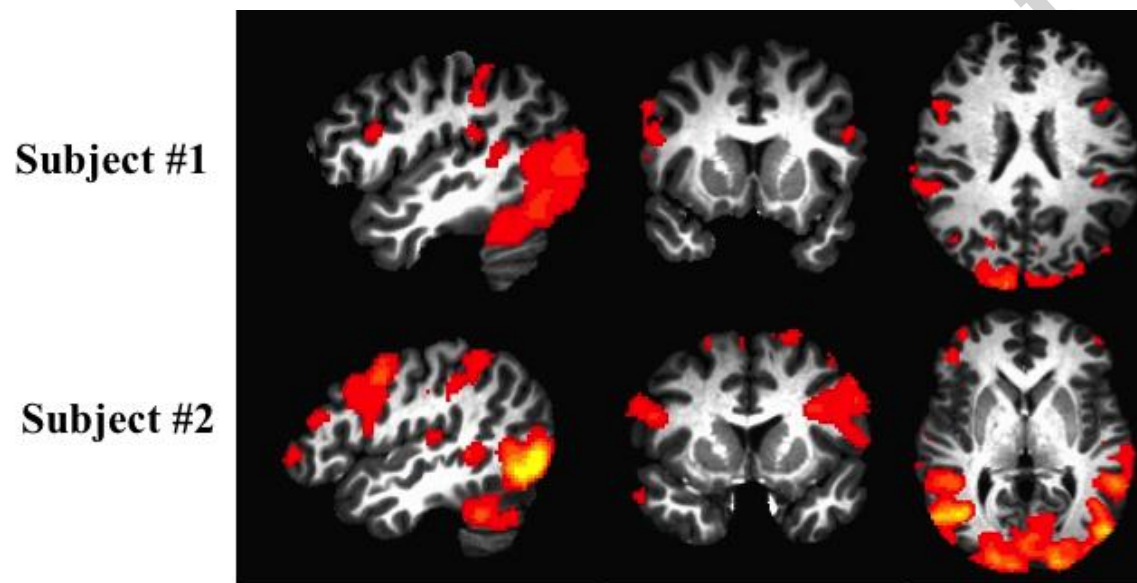


Table 1. Talairach coordinates for peak activations in the study.

Talairach coordinates for peak activations in the study

REGION	PEAK VOXEL			Approximate Brodmann Area	Cluster Size	T-score
	x	y	z			
Task Type						
Naming > Matching						
Left Superior Temporal Gyrus	-55	13	-4	22/44	3806	4.55
Left Precentral Gyrus	-37	-7	62	6	2447	4.54
Right Cerebellum	23	-41	-54		2362	4.27
Left Inferior Parietal Cortex	-67	-35	22	40	587	4.82
Right Parahippocampal Gyrus	27	1	-10		385	4.23
Left Superior Frontal Gyrus	-19	29	52	6/8	230	4.14
Right Superior Temporal Gyrus	53	11	-6	22	177	4.41
Cingulate Gyrus	-7	-27	38	31	119	4.34
Precuneus	-7	-61	54	7	113	4.16
Left Inferior Frontal Gyrus	-45	39	10	45/46	82	4.12
Left Cerebellum	13	-35	-50		80	4.19
Left Middle Frontal Gyrus	-37	47	26	9	72	4.21
Right Inferior Parietal Cortex	63	-27	34	40	57	4.16
Matching > Naming						
Cerebellum (and bilateral Occipital Cortex)	-1	-97	-2		6544	4.63
Right posterior Middle Temporal Gyrus	57	-47	6	21/22	182	4.49
Right anterior Middle Temporal Gyrus	61	-1	-12	21	119	4.37
Left Middle Temporal Gyrus	-53	-43	2		70	5.24
Sign Type						
Objects > Actions						
Left Thalamus	-3	-17	8		72	4.55
Left Middle Frontal Gyrus	-45	21	28	9	43	4.23

Table 2. Talairach coordinates for the peak voxel for regions of overlap in the matching and naming tasks and the number of individual subjects who showed activation in this area (total N=15).

REGION	Peak Voxel			Approximate Brodmann Area	Cluster Size	# Subjects Overlap
	x	y	z			
Cerebellum	-27	-55	-46		18900	15
cluster includes visual cortex bilaterally						15
cluster includes middle temporal cortex bilaterally						15
Right Inferior Frontal Gyrus	51	33	-6	BA 47	711	13
Left Inferior Frontal Gyrus	-49	19	0	BA 47	508	12
Left Inferior Frontal Gyrus	-43	39	4	BA 46	149	6
Left Inferior Parietal Cortex	-65	-31	28	BA 40	499	10
Left Parahippocampal Gyrus	-11	-21	-16		349	4
Left Angular Gyrus	-33	-53	34		230	3
Right Parahippocampal Gyrus	31	-15	-10		229	3
Right Supramarginal Gyrus	47	-53	40	BA 40	45	4

*p=.00025 was used (instead of p=.001) to get peak coordinates for the table in order to disconnect large contiguous regions.

Appendix

List of Stimuli

Action (verb)	Objects (noun)
call	phone
file	file
kick	football
read	book
shoot	handgun
sit	chair
blow dry	blow dryer
watch	television
write	pencil
calculate	calculator
crack egg	egg
dribble	basketball
drink	cup
iron	iron
light match	match
play guitar	guitar
swing racket	tennis
play violin	violin
roll dice	dice
shoot rifle	rifle
squeeze	lemon
take picture	camera
type	typewriter
swing bat	bat

highlight

- * We examine neural overlap of perception and production of American Sign Language (ASL) in native deaf signers using fMRI.
- * Deaf signers activated a network of language areas during perception and production of American Sign Language.
- * Neural overlap for perception and production of ASL was found in Broca's area, middle temporal and inferior parietal regions.