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Research Report
Neural correlates of human action observation in hearing and deaf subjects
**David Corina^{a,b,*}, Yi-Shiuan Chiu^{c,d}, Heather Knapp^a, Ralf Greenwald^a,
Lucia San Jose-Robertson^e, Allen Braun^e**
^aDepartment of Psychology, University of Washington, Seattle, USA^bCenter for Mind and Brain, University of California, Davis, USA^cDepartment of Psychology, Fu Jen Catholic University, Taipei, Taiwan^dLaboratories for Cognitive Neuroscience, National Yang Ming University, Taipei, Taiwan^eNational Institute on Deafness and Other Communication Disorders, National Institutes of Health, USA

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ABSTRACT

Accumulating evidence has suggested the existence of a human action recognition system involving inferior frontal, parietal, and superior temporal regions that may participate in both the perception and execution of actions. However, little is known about the specificity of this system in response to different forms of human action. Here we present data from PET neuroimaging studies from passive viewing of three distinct action types, intransitive self-oriented actions (e.g., stretching, rubbing one's eyes, etc.), transitive object-oriented actions (e.g., opening a door, lifting a cup to the lips to drink), and the abstract, symbolic actions-signs used in American Sign Language. Our results show that these different classes of human actions engage a frontal/parietal/STS human action recognition system in a highly similar fashion. However, the results indicate that this neural consistency across motion classes is true primarily for hearing subjects. Data from deaf signers shows a non-uniform response to different classes of human actions. As expected, deaf signers engaged left-hemisphere perisylvian language areas during the perception of signed language signs. Surprisingly, these subjects did not engage the expected frontal/parietal/STS circuitry during passive viewing of non-linguistic actions, but rather reliably activated middle-occipital temporal-ventral regions which are known to participate in the detection of human bodies, faces, and movements. Comparisons with data from hearing subjects establish statistically significant contributions of middle-occipital temporal-ventral during the processing of non-linguistic actions in deaf signers. These results suggest that during human motion processing, deaf individuals may engage specialized neural systems that allow for rapid, online differentiation of meaningful linguistic actions from non-linguistic human movements.

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* Corresponding author. 267 Cousteau Place, Davis, CA 95618, USA. Fax: +1 530 297 4400.
E-mail address: corina@ucdavis.edu (D. Corina).

1. Introduction

Interest in characterizing the neural systems and mechanisms involved in the perception of human actions has been fueled, in part, by recent studies of the macaque monkey. These papers report a unique neurophysiological response of a selective set of *mirror neurons*: cells which appear to couple the execution of goal directed actions with the perception of similar goal directed actions in another. In the original studies, a small population of these neurons was found to reside in a ventral premotor region (F5) (Gallese et al., 1996; Rizzolatti et al., 1996). Subsequent research has found neurons with mirror properties in area 7b (area PF of von Economo, 1929) of parietal cortex (Fogassi et al., 1998; Gallese et al., 2002). This F5-7b circuit in macaque, often referred to as the mirror–neuron circuit, is speculated to be part of a larger mirror–neuron system (Rizzolatti and Craighero, 2004) forming the biological basis for understanding a wide range of human actions including such complex behavioral constructs as imitation, social intent, empathy, and even human language (e.g., Rizzolatti and Arbib, 1998; Iacoboni et al., 1999; Rizzolatti et al., 2001; Arbib, 2003; Ferrari et al., 2003; Rizzolatti and Craighero, 2004).

Data from functional neuroimaging has been used to argue for a human homologue of a mirror–neuron system. A meta-analysis of PET data investigating the observation and imitation of hand actions (Grezes and Decety, 2001) identified a largely bilateral network that contributes to the action/perception pairings. This network includes the superior temporal sulcus, intraparietal sulcus, the inferior parietal lobule, and the premotor cortex. Functional MRI studies have further localized specialized cortical regions with properties that emulate those of mirror-like neurons. For example, Grezes et al. (2003) reported significant co-activation for executed and observed grasping in bilateral intraparietal sulcus, dorsal premotor cortex, superior temporal sulcus, and right parietal operculum (SII). In addition, activity was reported in the left ventral limb of the left precentral sulcus (BA 6) with extension to pars opercularis (BA 44) of the inferior frontal gyrus.

While a great deal of attention has been paid to identifying the anatomical loci that form the individual units of the mirror network, the functional mechanisms of this system are not as well understood. The sheer abundance of highly abstract functions now attributed or related to a frontal–parietal mirror–neuron system is impressive. Though theoretically parsimonious, the notion that a single cortical network mediates this wealth of behaviors, including language, is pragmatically challenging. For example, the notion of *resonance* is often used in the description of mirror responses in the nervous system. How this term relates to neural regions involved in action/perception pairings is largely unspecified. Other researchers have evoked forward and inverse models of sensorimotor control and perception as a possible theoretical construct in understanding mirror systems (Miall, 2003; Carr et al., 2003; Iacoboni and Zaidel, 2003). In this scheme, an inverse model describes the involvement of the STS, PF, and F5 in the perception of action, while a forward model linking F5 to PF to STS is used to generate predictions of movement outcome during imitated actions (Miall, 2003; Carr et al., 2003; Iacoboni, 2005).

Relevant to the current aims, it remains unclear whether a human mirror–neuron system is equally reactive to all forms of human actions. An early study by Grezes et al. (1999) has shown convincingly that the engagement of the human action recognition system may be modified both by the content of gestures observed (i.e., whether an action is known or unknown to the viewer) and by the intention of the subject while viewing the action (i.e., to watch an action with or without the goal of subsequent imitation). However, little is known about the specific correlates of different action types. Consider the following situations: An observer watches a person bring her hand to her mouth to act as a megaphone while shouting out the name of a child. In another instance, this same person brings her hand to her mouth to guard a sneeze. In yet another instance, the person has raised her hand, holding an ice-cream cone, to her mouth. In a fourth instance the hand is brought into contact with the chin in a conventionalized manner: the arbitrary combined configurations of hand, mouth, and motion type signaling the concept “mother” in American Sign Language (ASL). Does a human action/mirror system become equivalently engaged by each of these instances of distinct action classes?

In the present study, we sought to determine whether the focus and extent of neural activity during passive viewing of human actions is modulated as a function of the type of human action observed and the experience of the viewer. We examined the perception of three classes of actions (self-oriented, object-oriented, and communicative) in two groups of subjects (hearing individuals unfamiliar with signed language and deaf users of signed language). The three classes of action were chosen to reflect increasing degrees of meaningfulness. Self-oriented actions, such as scratching one’s head or rubbing one’s eyes, are highly frequent and may not trigger conceptual elaboration. Impressionistically, in everyday interactions one tends to “look past” these gestures, perhaps because they are largely irrelevant for the viewer. Object-oriented actions (throwing a ball, folding a shirt, etc.) may be considered goal-directed actions that have clear, highly specific, and predictable functional consequences. Finally, gestures used in manual signing systems of the deaf, such as American Sign Language (ASL), are clearly communicative in nature even for individuals who are not users of signed languages.

For deaf individuals who use a visual–manual language as their primary form of communication, the successful perception of each of these types of human motion is especially vital. Not only must signers be attuned to the usual plethora of non-linguistic actions produced by those around them, they must also be able to quickly detect the presence of linguistic movements produced by fellow signers. This entails being able to parse sign language motions from other kinds of human movements that co-occur in the visual environment and map these sign language actions to linguistic movement patterns stored in memory.

A growing literature reports that the perception of signed and spoken languages engages left hemisphere perisylvian, inferior frontal, and posterior temporal–parietal regions. In addition, some studies have shown a greater role for right hemisphere regions in sign comprehension (Neville et al., 1998; Bavelier et al., 1998; Newman et al., 2002; for recent reviews, see Corina, in press; Corina and Knapp, 2006).

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