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Research paper

Neural bases of action abstraction

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ABSTRACT

There has been recent debate over whether actions are processed primarily by means of motor simulation or cognitive semantics. The current study investigated how abstract action concepts are processed in the brain, independent of the format in which they are presented. Eighteen healthy adult participants viewed different actions (e.g., diving, boxing) in the form of verbs and schematic action pictograms while functional magnetic resonance imaging (fMRI) was collected. We predicted that sensorimotor and semantic brain regions would show similar patterns of neural activity for different instances of the same action (e.g., diving pictogram and the word 'diving'). A representational similarity analysis revealed posterior temporal and sensorimotor regions where specific action concepts were encoded, independent of the format of presentation. These results reveal the neural instantiations of abstract action concepts, and demonstrate that both sensorimotor and semantic systems are involved in processing actions.

1. Introduction

How do we understand and conceptualize actions? Using neuroimaging studies, researchers attempt to explain how the human brain processes actions—whether they are performed, observed, or represented by words or other symbols. Some researchers theorize that actions are processed by engaging our own sensorimotor networks—in other words, that we understand actions by vicariously simulating perceptual, sensory, and motor states associated with an action (Barsalou, 2008; Gallese & Sinigaglia, 2011; Rizzolatti & Sinigaglia, 2010). This view is closely tied to the mirror neuron theory of embodied action understanding (Gallese, 2013; Rizzolatti & Sinigaglia, 2010) according to which similar neural systems are active whether an action is observed or performed. Other theories of action understanding hold that action simulation is not a primary mode of action understanding, but rather that actions are processed cognitively—i.e., that they are categorized and accessed without reliance on the motor system (Wurm, Ariani, Greenlee, & Lingnau, 2015; Wurm & Lingnau, 2015).

Simulation theories of action comprehension postulate that actions are understood through vicarious activation of the motor system. This simulation can take two forms. Actions can be understood in terms of how the observer would herself carry out the action. Such "action implementation" (Quandt & Chatterjee, 2015) is largely reliant on dorsal streams, including frontal and parietal regions such as the premotor cortex (Michael et al., 2014), primary sensorimotor cortices, and the posterior parietal lobe. From the action simulation viewpoint, the regions of the brain involved in understanding actions are the same neural circuits that instantiate the motor and sensory features of actions (Avenanti, Candidi, & Urgesi, 2013). Similarly, actions can also be understood by simulating memories of having observed them. In this case we expect that neural circuits in or adjacent to visual motion area MT + would be engaged. There is evidence for action simulation throughout the motor systems in regions including the supplementary motor area, primary somatosensory cortex, premotor cortex, the supramarginal gyrus, and the superior parietal lobe (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Grezes & Decety, 2001).

Other brain regions process actions as cognitive semantic entities rather than by means of simulation, and these regions may also process other categories (e.g., objects or animals) in a similar manner. In this cognitive action semantics framework, posterior regions near the visual system, such as the lateral occipital cortex (LOC), and the posterior middle temporal gyrus (pMTG), along with inferior parietal regions are generally considered to be hubs of action representation (Leshinskaya & Caramazza, 2015; Wurm & Lingnau,2015). For example, the inferior posterior parietal cortex (Binder, Desai, Graves, & Conant, 2009) and the MTG (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Wu, Morganti, & Chatterjee, 2008) are associated with conceptual action associations, while the IFG (Thompson-Schill et al., 1998) and anterior temporal lobes are associated with domain-general semantic processing (Abel et al., 2015). pMTG has been shown

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to be causally involved in action understanding in patient studies (Urgesi, Candidi, & Avenanti, 2014; Wu, Waller, & Chatterjee, 2007).

While these two frameworks are sometimes pitted against one another, they are not mutually exclusive. Some meta-analyses of action processing demonstrate that both the simulation and the cognitive model of action processing are involved in action processing, depending on the task, the stimuli, and one's experience with a given action. One such meta-analysis identified regions that are uniquely activated by the observation of actions (Caspers, Zilles, Laird, & Eickhoff, 2010). This analysis revealed that action observation involved both traditional "mirror system" regions (premotor cortex, IPL, primary somatosensory cortex) and also the supplementary motor area, pMTG, and extrastriate visual area. Another meta-analysis identified the left supramarginal gyrus and the left pMTG as subserving "action semantics" (Binder et al., 2009). Notably, a recent meta-analysis identified regions involved in conceptual action processing of action words and pictures (Watson, Cardillo, Ianni, & Chatterjee, 2013).

Temporal cortex regions adjacent to the visual motion area (MT+) and inferior and superior parietal regions were implicated in conceptual action representations. Along the left lateral temporal cortex, a gradient of abstraction was found, with more abstract action representations housed in more anterior parts of the posterolateral temporal lobe. While these meta-analyses provide important starting points for approaching the question of conceptual action processing, they are inherently limited to explaining specific types of experimental stimuli. For instance, the meta-analysis conducted by Watson et al. (2013) included studies that used static depictions of action (e.g., line drawings), but excluded action execution (e.g., participants producing actions) and moving stimuli. Additionally, meta-analyses typically use whole-brain analyses, which identify common activations, but do not directly test specific hypotheses.

Most action-related experiments identify brain regions that process actions when presented in a specific format. For instance, a study might ask participants to view action videos (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Kirsch & Cross, 2015; Quandt & Marshall, 2014; Wurm et al., 2015), static action pictures (Kourtzi & Kanwisher, 2000; Kable, Lease-Spellmeyer, & Chatterjee, 2002; Watson, Cardillo, Bromberger, & Chatterjee, 2014), or action words (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Papeo & Lingnau, 2015; Willems, Toni, Hagoort, & Casasanto, 2010). While these studies contribute to the understanding of how we process actions presented in a certain format, they are limited in their ability to answer the broader question: what regions of the brain are involved in processing actions, regardless of the format in which they're presented? For instance, what brain systems process the format-independent concept of "boxing", rather than simply the English word *boxing* or a video of a person boxing?

This question of how the brain processes format-independent information can be addressed experimentally, in part thanks to advances in functional neuroimaging analysis techniques. By examining similarities in the neural response to different versions of a concept, one can make inferences about processing in the brain that is common to different instances of the same concept, rather than simply comparing neural activity in response to different stimuli. Researchers have identified brain regions involved in processing format-independent conceptualizations of objects (Devereux, Clarke, Marouchos, & Tyler, 2013; Fairhall & Caramazza, 2013), distances (Parkinson, Liu, & Wheatley, 2014), and letters (Rothlein & Rapp, 2014). In these studies, neural activity during one condition (e.g., viewing object nouns) is correlated with neural activity during another condition (e.g., viewing object images) to see which brain regions have similar responses to different formats of the same object concept (e.g., "cup").

A critical issue in the action processing literature concerns the format of the actions in question. A given action may be seen in real life (e.g., watching someone throw a ball), or may be referred to by representational means, such as an action verb or a picture of an action. Different formats of action-related stimuli vary in their levels of abstraction. For instance, a high-definition video feed of a football game is richly detailed, and is not particularly abstract, other than being rendered on a flat screen. On the other hand, the word "football" is a symbolic, and highly abstract, representation of the same action concept. One intermediate mode of representing actions is schematic pictograms of action, such as line drawings or stick figures like those used to identify sports during the Olympic games. These are intermediate in the sense that they share some symbolic properties of words and some analog properties of pictures (Amorapanth et al., 2012; Chatterjee, 2001; Kranjec, Ianni, & Chatterjee, 2013). Schematic representations of spatial relations may be the foundation upon which we understand abstract spatial information. Unlike pictures, they are abstract by virtue of being types rather than tokens of actions or relations. Unlike words, they are understood easily and are less subject to cultural variations. For instance, a left-facing arrow conveys spatial direction more readily than the word "left". Such image schemas (e.g., arrows, lines, or circles representing abstract concepts) may provide a structure that allows us to conceptualize more complex relations between abstract entities (Lakoff & Johnson, 1999; Talmy, 1983). Schematic representations of spatial relations may especially rely on the right supramarginal gyrus (Amorapanth et al., 2012). Other recent work demonstrates that symbolic stimuli preferentially activate the left inferior frontal gyrus (Muayqil, Davies-Thompson, & Barton, 2015).

We aimed to investigate the format-independent processing of actions, by examining the neural processing common to different formats of action stimuli: lexical and schematic action representations. Action schemas preserve the fundamental structure of action concepts, while abstracting away perceptually-rich details present in a less symbolic format, such as a color photograph or a video (Chatterjee, 2001). By examining the similarities in action processing evoked by schematic action images and action words, we characterize the regions of the brain involved in format-independent conceptual action processing (Barsalou, 2008). We designed a functional neuroimaging study in which we showed participants schematic action images and corresponding verbs. We then conducted a representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008) in order to test the hypothesis that format-independent action processing would evoke neural activity in brain regions devoted to motor and sensory simulation of these actions as well as brain regions implicated in associative processes (Quandt & Chatterjee, 2015).

2. Materials and methods

2.1. Participants

Twenty participants (12 females; mean age = 25.79, SD = 5.23) volunteered to participate in the study in exchange for monetary compensation. All participants gave their informed consent before participation, and none reported history of neurological abnormality. All were right-handed and native speakers of English. Two participants were excluded from all analyses because of excessive movement throughout data acquisition, for a final sample of eighteen (11 females).

2.2. Stimuli

Four classes of stimuli were created: action pictograms, object pictograms, action words, and object words. All stimuli were presented in black on a white background in E-Prime 2.0. Action pictograms consisted of six schematic images depicting actions (boxing, diving, golfing, fencing, skating, and skiing), taken from the set of 1972 Olympic pictograms designed by Otl Aicher (bottom of Fig. 1; Aicher, 1976). These copyrighted images were used with permission from ERCO GmbH (© 1976 by ERCO GmbH, Lüdenscheid, Germany). The six object pictograms (globe, telescope, beehive, beaker, shoe, teapot; Fig. S1 in Supplemental Materials) included some images from the Aicher pictogram