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The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system

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Verbs have two separate levels of meaning. One level reflects the uniqueness of every verb and is called the "root". The other level consists of a more austere representation that is shared by all the verbs in a given class and is called the "event structure template". We explore the following hypotheses about how, with specific reference to the motor features of action verbs, these two distinct levels of semantic representation might correspond to two distinct levels of the mirror neuron system. Hypothesis 1: Root-level motor features of verb meaning are partially subserved by somatotopically mapped mirror neurons in the left primary motor and/or premotor cortices. Hypothesis 2: Template-level motor features of verb meaning are partially subserved by representationally more schematic mirror neurons in Brodmann area 44 of the left inferior frontal gyrus. Evidence has been accumulating in support of the general neuroanatomical claims made by these two hypotheses—namely, that each level of verb meaning is associated with the designated cortical areas. However, as yet no studies have satisfied all the criteria necessary to support the more specific neurobiological claims made by the two hypotheses—namely, that each level of verb meaning is associated with mirror neurons in the pertinent brain regions. This would require demonstrating that within those regions the same neuronal populations are engaged during (a) the linguistic processing of particular motor features of verb meaning, (b) the execution of actions with the corresponding motor features, and (c) the observation of actions with the corresponding motor features.

1. Introduction

Many traditional approaches to the human conceptual system assume that semantic knowledge is represented separately from, and is qualitatively different than, modality-specific systems for perception, action, and emotion (e.g., Barsalou & Hale, 1993; Fodor, 1975; Landauer & Dumais, 1997; Pylyshyn, 1984; Smith, 1978). According to this classic "disembodied cognition hypothesis" (Mahon & Caramazza, 2008), sensorimotor and affective representations are transduced into amodal structures such as feature lists, semantic networks, frames, etc., and cognitive processes operate on those structures, not on memories of the original experiences. Moreover, the content of all types of concepts, including those encoded by words, is believed to consist entirely of combinations of these abstract symbols.

A very different line of thinking is currently being pursued by a growing number of researchers in linguistics (e.g., Bergen, 2007; Evans & Green, 2006; Hampe, 2005), philosophy (e.g., Prinz, 2005; Gallagher, 2005; Johnson, 2007), psychology (e.g., Barsalou, 2008b; Gibbs, 2006; Pecher & Zwaan, 2005; Klatzky, MacWhinney, & Behrmann, 2008), and neuroscience (e.g., Barsalou, 2008a, 2008c; Haggard, Rossetti, & Kawato, 2007; Jeannerod, 2006; Kemmerer, in press; Keysers & Gazzola, 2006; Martin, 2007), all of whom endorse one form or another of what is often called the Embodied Cognition Framework (also known as the Grounded Cognition Framework or the Simulation Framework). The central tenet of this approach is that semantic knowledge is not purely amodal, but is instead anchored in modality-specific input/output systems, such that many forms of conceptual processing involve the transient recapitulation of diverse aspects of sensorimotor and affective experiences. As emphasized recently by Hoenig, Sim, Bochev, Herrnberger, and Kiefer (2008) and Kemmerer (in press), the notion of modality-specific semantic maps does not rule out the possibility of higher-order integrative memory systems that contain systematically organized "conjunctive units" for binding cross-modal feature correlations; indeed, there is accumulating evidence that, at least for certain kinds of object concepts, integrative systems of this nature may reside in the temporal poles

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(e.g., Bright, Moss, Longe, Stamatakis, & Tyler, 2007; Lambon Ralph, Pobric, & Jefferies, in press; Patterson, Nestor, & Rogers, 2007). The most important, and most controversial, claim of the Embodied Cognition Framework, however, is that these integrative systems are not by themselves sufficient for full-fledged conceptual processing; rather, such processing requires that the abstract conjunctive units within the integrative systems activate, in top–down fashion, modality-specific representations that "flesh out", to varying degrees, the contextually most appropriate concrete content of the relevant ideas (Damasio 1989a, 1989b, 1989c; Simmons & Barsalou, 2003).

In recent years a great deal of research within the Embodied Cognition Framework has focused on the nature of action concepts, and this is due in large part to the seminal—some would even say "paradigm-shattering" (Ramachandran, 2008)—discovery of mirror neurons nearly 20 years ago (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). These are cells that discharge not only when certain kinds of actions are executed by the self, but also when they are seen or heard being performed by someone else. Thus, mirror neurons appear to represent behavioral patterns per se, and because they neutralize the self–other distinction,[1] they may turn out to have profound implications for intersubjective understanding (Hurley, 2008; Iacoboni, 2008). Owing to their remarkable response properties, these cells seem to confirm a prescient statement made by an early advocate of the Embodied Cognition Framework, namely William James (1890, p. 526): "Every representation of a movement awakens in some degree the actual movement which is its object".

Mirror neurons have been found in a variety of brain regions, but before briefly reviewing those results we would first like to clarify our terminology. There is currently some disagreement over the definition of "mirror neurons". Cells that fire during both action execution and action observation were first discovered in area F5 of the macaque ventral premotor cortex, and this region has continued to received a great deal of attention over the years. Apparently for this purely historical reason, however, some researchers seem to think that only F5 cells deserve to be called "mirror neurons", and that cells in other cortical areas that also fire during both action execution and action observation do not qualify. For example, after providing compelling evidence that cells with mirror-like properties—i.e., cells that achieve action observation-execution matching—are broadly distributed across many sectors of the macaque frontal cortex, Raos, Evangeliou, and Savaki (2007, p. 12682) conclude that their results "undermine the 'mirror neuron system' concept", and that the more general notion of "mental simulation" is explanatorily superior because it, rather than the former concept, "assigns the role of understanding others' actions to the entire distributed neural network, which is responsible for the execution of actions". The same research team recently expressed essentially the same view after extending their work to multiple sectors of the macaque parietal cortex (Evangeliou, Raos, Galletti, & Savaki, in press). We believe, however, that "mirror neurons" should be defined by functional rather than anatomical criteria. Indeed, this perspective is adopted in several prominent reviews of the mirror neuron system which indicate that the system is not necessarily limited to F5 (Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001).

Having said that, we consider it noteworthy that in the macaque brain mirror neurons have already been found in an impressively large number of areas:

- ventral premotor cortex (di Pellegrino et al., 1992; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Keysers et al., 2003; Kohler et al., 2002; Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005; Raos et al., 2007; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996);
- dorsal premotor cortex (Cisek & Kalaska, 2004; Raos et al., 2007);
- primary motor cortex (Raos, Evangeliou, & Savaki, 2004; Raos et al., 2007; Tkach, Reimer, & Hatsopoulos, 2007);
- several medial frontal regions (Raos et al., 2007);
- inferior parietal cortex (Fogassi et al., 2005; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002; Evangeliou et al., in press);
- superior parietal cortex (Evangeliou et al., in press);
- primary and supplementary somatosensory areas (Evangeliou et al., in press).

There is mounting evidence that mirror neurons also exist in a wide range of human brain areas. Despite some important limitations that we address later (Mahon & Caramazza, 2005, 2008; Negri et al., 2007; Turella, Pierno, Tubaldi, & Castiello, 2009), numerous human brain mapping studies suggest that the visual or auditory perception of an action engages many of the same neural networks that are recruited during its execution—a remarkable phenomenon which suggests that understanding other people's actions may involve, to some degree, simulating them in a completely automatic, unconscious manner (we discuss some of this literature in Sections 3.1 and 4.1).

In addition, a growing literature suggests that, as predicted by the Embodied Cognition Framework, when people understand linguistic descriptions of actions, motor-related regions in their frontal lobes are engaged (for reviews see Fischer & Zwaan, 2008; Pulvermüller, 2005, 2008; Willems & Hagoort, 2007). So far, linguistically triggered motor resonance has not been investigated in as much detail as the type of motor resonance that is induced by action observation, but there is increasing interest in the provocative idea that comprehending a linguistic description of an action might involve covertly recapitulating the type of action that it refers to, using some of the same brain systems that underlie the execution and observation of that type of action. As yet, however, this line of research has, for the most part, neglected recent advances in linguistic theory, especially regarding the lexical and grammatical encoding of action. The main purpose of this paper is therefore to take some steps toward filling that gap.

In particular, our aim is to explore some possible connections between, on the one hand, the Embodied Cognition Framework as it has hitherto been applied to action concepts and the mirror neuron system, and on the other hand, the Two-Level Theory of verb meaning, which is an approach to analyzing the linguistic representation of action that has not only been supported and refined for over 20 years (for a review see Levin & Rappaport Hovav, 2005), but has also arguably led to deep insights about the fabric of human thought (Pinker, 2007). Basically, the Two-Level Theory holds that verb meanings have two separate levels of structure—one for the "root" or "constant" semantic features that characterize individual verbs, and another for the "event structure templates" or "thematic cores" that are shared by all the verbs in a given class. In Section 2 we elaborate this central claim of the theory in greater detail. Then in Sections 3 and 4 we explore the following hypotheses about how, with specific reference to the motor features of action verbs, the two distinct levels of semantic representation might correspond to two distinct levels of the mirror neuron system:

Hypothesis 1. Root-level motor features of verb meaning are partially subserved by somatotopically mapped mirror neurons in the left primary motor and/or premotor cortices.

[1] See Jeannerod (2007) and Tsakiris, Schütz-Bosbach, and Gallagher (2007) for two among several current theories of how the self-other distinction is ultimately achieved with respect to the production and perception of actions.