Embodied Cognition and Mirror Neurons: A Critical Assessment

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Abstract

According to embodied cognition theories, higher cognitive abilities depend on the reenactment of sensory and motor representations. In the first part of this review, we critically analyze the central claims of embodied theories and argue that the existing behavioral and neuroimaging data do not allow investigators to discriminate between embodied cognition and classical cognitive accounts, which assume that conceptual representations are amodal and symbolic. In the second part, we review the main claims and the core electrophysiological findings typically cited in support of the mirror neuron theory of action understanding, one of the most influential examples of embodied cognition theories. In the final part, we analyze the claim that mirror neurons subserve action understanding by mapping visual representations of observed actions on motor representations, trying to clarify in what sense the representations carried by these neurons can be claimed motor.

Contents

INTRODUCTION

Over the past 25 years, numerous theories have been proposed that emphasize the role of perceptual and motor processes for higher cognitive abilities such as language comprehension and action understanding. According to these theories, which we broadly group under the term embodied cognition theories, higher cognitive abilities are achieved in large part or entirely through the reenactment of processes used primarily for sensory input processing or for action execution. This review aims to critically evaluate the central tenets of embodied cognition theories by considering some of the most significant examples of such theories and the evidence supporting them.

Although there are many flavors and varieties of embodied cognition theories, the vast majority of them agree on at least two claims (e.g., Barsalou 2008, Gallese & Lakoff 2005). First, they all converge on the claim that semantic knowledge is carried by sensorimotor representations: The neural systems that are causally involved in forming and retrieving semantic knowledge are the same systems necessary for perceiving different sensory modalities or for producing actions. In line with this claim, studies have proposed that retrieving semantic knowledge of perceptual properties such as the colors of objects critically depends on the neural systems implicated in the perception of these properties (in this example, color perception; Simmons et al. 2007) and that understanding another person's actions requires the contribution from one's own motor system (Rizzolatti & Sinigaglia 2010). Second, most embodied cognition theories emphasize the importance of simulation in conceptual processing (Jeannerod 2001, Zwaan & Taylor 2006). On this account, retrieving semantic knowledge requires neural systems that are involved in perception or action execution and also requires that they perform the same processes utilized during perception or action execution. Semantic processing amounts to a reenactment of stored modality-specific representations in the relevant sensorimotor cortices. For instance, all the semantic knowledge we have about chairs could be exhaustively described as a collection of interacting modality-specific records of what a chair looks like, of the action of sitting, of the somatosensory experiences associated with sitting in a chair, etc. (Barsalou 2008). In this review, we focus on the evidence that investigators have used to support the validity of these two claims.

In both the behavioral and neuroimaging literatures, the arguments offered in support of embodiment are based on numerous interesting findings. However, investigators do not agree on whether the findings actually provide support to the central claims of embodied cognition (Barsalou 2008, Fischer & Zwaan 2008, Glenberg & Kaschak 2002, Kiefer & Pulvermüller 2012) or whether they are orthogonal to such claims, that is, consistent with classical, nonembodied theories of cognition (Caramazza et al. 1990, Chatterjee 2010, Csibra 2008, Jacob & Jeannerod 2005, Mahon & Caramazza 2008). Here we refer to the latter theories as cognitive theories. In the first part of this review, we attempt to clarify the nature of the controversy by presenting the neuroimaging and behavioral results that have been cited in support of embodied theories of semantic knowledge, and we discuss the alternative, cognitive interpretations of these results from the literature. Even though our discussion in this part centers on semantic knowledge, we emphasize that the issues at the core of the controversy are analogous to those in other contexts.

The remainder of the review is then devoted to a critical evaluation of perhaps the most influential embodied theory of cognition: the mirror neuron theory. Mirror neurons were originally discovered in the premotor cortex of the macaque monkey and are characterized by responses produced not only when the animal performs an action but also when it observes a similar action (di Pellegrino et al. 1992, Gallese et al. 1996). For instance, the same neuron would fire at an increased rate both when the monkey grasps an object with its hand and when it passively observes the object being grasped by the hand of the experimenter. This intriguing property inspired a theory that postulates a causal involvement of such motor neurons in action understanding (mirror neuron theory). We review the theory and point to the aspects of the theory that remain debated. In particular, we discuss whether there is sufficient evidence to show that mirror neurons play a causal role in action understanding, and we evaluate the direct-matching hypothesis (one of the central tenets of the mirror neuron theory) in light of the available evidence. Finally, we analyze the central claim that mirror neurons subserve action understanding through the reenactment of motor representations, trying to clarify in what sense the representations carried by mirror neurons can be claimed motor. [For a critical assessment of embodied theories of decision making, see Freedman & Assad (2011)].

EMBODIED COGNITION THEORIES: THE NATURE OF THE CONTROVERSY

Embodiment and Semantic Knowledge: Neuroimaging Studies

A central claim of embodied cognition states that semantic knowledge is represented in sensorimotor systems (Buccino et al. 2005; Goldberg et al. 2006; Pulvermüller et al. 2000, 2005; Simmons et al. 2005, 2007). Numerous studies looked for an overlap between brain areas involved in sensorimotor processes and those involved in the retrieval of semantic knowledge (Hauk et al. 2004, Postle et al. 2008, Simmons et al. 2007; for a recent meta-analysis, see Watson et al. 2013). If semantic knowledge were represented in sensorimotor areas, those areas should be active during sensorimotor processing as well as during retrieval of semantic knowledge. This prediction has been tested for color knowledge and action word comprehension.

The Case of Color Knowledge

Simmons et al. (2007), using fMRI, found evidence for an overlap between areas involved in color perception and those involved in the retrieval of color knowledge. The authors first individuated areas involved in color perception by contrasting activity during a color-discrimination task with activity during a task discriminating between hues of gray. Then, within these areas, they tested whether the activity during retrieval of color knowledge (e.g., TAXI = yellow) was greater than that during a control task requiring subjects to evaluate whether a particular motor property was associated with an object (e.g., HAIR = combed). The authors found a greater signal for the color knowledge task than for the control task in a left fusiform area demonstrated to be more active during color perception than during discrimination of hues of gray. They concluded that this result supported embodied theories of color knowledge. However, their conclusion was too strong. An overlap between brain areas active in two different tasks does not imply an overlap between the neural mechanisms involved in performing those tasks. Several neural populations coexist in a single brain area, and the results cannot rule out that the observed overlap derives from the activity of two different, nonoverlapping networks of neurons (see also Dinstein et al. 2008). Furthermore, cognitive theories of conceptual representation also predict some overlap between activity noted during color perception and that shown during the retrieval of color knowledge. According to cognitive theories, some representations of color do not depend on the specific modality through which the information is accessed, that is, those that are activated when one hears a color word, when one thinks of a color, and when one sees a color. Therefore, these representations would also be active during both color perception and retrieval of color knowledge.

The findings reported by Simmons et al. (2007) may actually be problematic for embodied theories of color knowledge. The double dissociation between color discrimination and color knowledge in cases of brain damage has been well documented (Miceli et al. 2001), ruling out the strong embodied view that would reduce color knowledge entirely to reactivations of mechanisms used primarily for color discrimination. The overlap detected by Simmons et al. (2007) does not occur in areas involved in relatively early stages of color processing (lingual gyrus), as determined by lesion overlap analyses of deficits in color perception (Bouvier & Engel 2006). Instead, and in accord with cognitive theories, the overlap occurs more anteriorly (left fusiform gyrus), in areas that, when damaged, do not affect color perception but impair retrieval of object color knowledge (Miceli et al. 2001).

The Case of Action Words

Another prominent embodied theory in the contemporary literature concerns the understanding of the meaning of action words, which is assumed to depend on the reenactment of motor processes involved in performing those actions (Pulvermüller 2005). The results of many studies have been interpreted to support this theory (Aziz-Zadeh et al. 2006, Boulenger et al. 2009, Pulvermüller et al. 2006, Tettamanti et al. 2005). Here, we discuss a typical example.

In an fMRI study, Hauk et al. (2004) investigated participants' brain activity during passive reading of hand, foot, and mouth action words (e.g., pick, kick, lick) and during the performance of actions with the corresponding body parts. They found that passive reading of action words activates premotor and frontal areas in a somatotopic manner. However, the study did not report a direct analysis of the overlap between the activity in the word and the motor localizer conditions. Although the activity during the two different conditions seems to partially overlap for some effectors, many of the areas of activity during the two conditions are markedly different; therefore, it is difficult to assess whether and to what extent the activations in the two tasks overlap. Nonetheless, the authors interpreted the results as support for the embodied view of action word processing (for similar studies and conclusions, see Aziz-Zadeh et al. 2006, Boulenger et al. 2009, Pulvermüller et al. 2006, Tettamanti et al. 2005).

However, somatotopic activity during action word processing is not by itself evidence supporting an embodied theory of action processing. As we have discussed in the case of color, overlap is predicted by embodied theories, but it is also predicted by nonembodied theories of cognition. Therefore, even in the presence of an overlap, we must ask where the area of overlap is located. Postle and colleagues (2008) investigated the overlap between areas involved in action execution and areas involved in understanding action words more rigorously, and they failed to find reliable somatotopic recruitment of the primary or premotor cortex during the processing of action words (for similarly problematic results, see de Zubicaray et al. 2013, Kemmerer et al. 2008, Kemmerer & Gonzalez-Castillo 2010, Lorey et al. 2013). A recent meta-analysis of fMRI studies on action concepts found no support for the idea that the activation of premotor and motor regions plays a significant role in processing action concepts (Watson et al. 2013; see also Bedny & Caramazza 2011).

In a series of studies, Pulvermüller and colleagues tried to support the embodied view of action word understanding, arguing that when participants read action words their motor cortex is activated rapidly (within 200 ms) and somatotopically (Hauk & Pulvermüller 2004; Pulvermüller et al. 2000, 2005). However, these findings do not address whether such fast and somatotopic activation plays a causal role in semantic processing or is merely the consequence of semantic processing in other, nonmotor areas (Mahon & Caramazza 2008). Studies that used transcranial magnetic stimulation (TMS) over the precentral motor cortex to assess its causal role in semantic processing of action words (Buccino et al. 2004, D'Ausilio et al. 2009, Gerfo et al. 2008, Mottonen & Watkins 2009, Papeo et al. 2009, Willems et al. 2011) have produced inconsistent results (for a review, see Papeo et al. 2013). In contrast, a recent study that used repetitive TMS to interfere with processing in the left posterior middle temporal gyrus (lpMTG), an area known to represent action verb semantics (Peelen et al. 2012), eliminated the action–nonaction verb distinction in the precentral motor cortex (Papeo et al. 2014). This result suggests that activity in the precentral motor cortex during action word comprehension is driven by semantic processing in lpMTG.

In sum, as in the case of color knowledge, the overlap between sensorimotor mechanisms and semantic knowledge does not seem to occur within areas involved in low-level sensorimotor processing, and the activity in precentral motor areas is driven by semantic processing outside the motor system.

Embodiment and Semantic Knowledge: Behavioral Findings

A wide range of behavioral evidence has been produced supporting the claims of embodied cognition theories. All of these studies follow the same general pattern in that they demonstrate various interactions between semantic knowledge and sensorimotor processes. Such interactions are then interpreted as evidence that sensorimotor processes or simulation plays a central role in mediating semantic knowledge.

The relevant evidence comes from various domains. For instance, Hansen et al. (2006) observed that one can sometimes perceive achromatic objects as having a color and that the perceived color is systematically related to the canonical color of the object (e.g., yellow for a banana). These data have been taken to suggest that observers automatically simulate the canonical color of an object as they categorize it. The effects of objects' perceptual properties can become apparent even in tasks that involve a substantial amount of semantic processing. Stanfield & Zwaan (2001) and Zwaan et al. (2002) have shown that in a picture-naming paradigm subjects name an object more quickly if it is preceded by text that implies perceptual properties that match those in the object's depiction. For example, subjects name a picture of an eagle with outstretched wings faster compared with a picture of an eagle with folded wings if the former is preceded by the sentence, "The ranger saw the eagle in the sky." Embodied cognition theory proposes that in order to understand the sentence, subjects simulate the perceptual processes implied by its meaning and are therefore faster at naming a perceptually congruent picture.

Studies have shown similar facilitation effects with other experimental paradigms in the perceptual domain (e.g., Borghi et al. 2004, Bosbach et al. 2005, Meteyard et al. 2008, Solomon & Barsalou 2004) but also in the motor domain (Gentilucci & Gangitano 1998, Glenberg & Kaschak 2002). For example, participants are faster to respond to target words (e.g., "typewriter") following prime words referring to objects that, if manipulated in a typical way, require a similar motor response (e.g., "piano") (Myung et al. 2006; but see Postle et al. 2013). And Rueschemeyer et al. (2010) found that prior planning of motor actions facilitates processing of words denoting objects typically associated with such actions. These results, as explained by embodied cognition theories, are taken to suggest that at least some aspects of semantic knowledge about words and objects are stored in the form of motor representations.

Even though such behavioral evidence is of great interest in its own right, it plays only a very limited role in assessing the two central claims of embodied cognition theories. In particular, the interactions between semantic knowledge and sensorimotor processes do not address whether sensorimotor processes are, in fact, necessary for mediating conceptual representations. Cognitive, nonembodied accounts of semantic knowledge also predict such interactions; however, on these accounts, sensorimotor processes are triggered by retrieving semantic knowledge through association. For example, when one hears the sentence "The ranger saw the eagle in the sky," it is perfectly plausible that one retrieves a visual representation of a flying eagle and is therefore primed to name the picture of a flying eagle faster than a picture of a standing eagle. However, in this case, the activation of sensorimotor representations is a consequence of retrieving semantic knowledge rather than an integral part of it (Chatterjee 2010, Mahon & Caramazza 2008). The mere fact that sensorimotor processes interact with retrieval of semantic knowledge provides no clue about the direction of the causal link between the two. Thus, extant behavioral data do not allow one to discriminate between embodied and cognitive accounts.

THE MIRROR NEURON THEORY OF ACTION UNDERSTANDING

The mirror neuron theory has been immensely influential both as the most complete instantiation of an embodied cognition theory in one particular domain, action understanding, and as the foundation for embodied cognition theories in many other domains, such as language and social cognition. Below, we review the theory's main claims; the core evidence cited as supporting those claims, which stem from monkey physiology and human studies; and some of the problematic issues that some researchers have raised.

Main Claims of the Mirror Neuron Theory

Since its original formulation, several different versions of the mirror neuron theory have been put forth. The basic claim, which has not changed substantially across its various versions, concerns the overlap of neural mechanisms mediating action understanding and action production. It is most clearly expressed in a review by Rizzolatti et al. (2001). These authors maintain that "we understand actions when we map the visual representation of the observed action onto our motor representation of the same action. According to this view, an action is understood when its observation causes the motor system of the observer to resonate. So, when we observe a hand grasping an apple, the same population of neurons that control the execution of grasping movements becomes active in the observer's motor areas. By this approach, the motor knowledge of the observer is used to understand the observed action" (Rizzolatti et al. 2001, p. 661).

The neurons that are active, for instance, both when an individual grasps an apple and when the individual observes someone else grasp an apple are, by definition, mirror neurons. The theory in effect asserts that these neurons constitute a key mechanism shared by action production and action understanding. More specifically, it suggests that populations of mirror neurons are causally involved in mediating both these functions.

The presence of a mechanism that is recruited during both production and understanding does not distinguish the mirror neuron theory from classical cognitive theories according to which central, abstract representations are involved in both comprehension and production of actions and language. However, the mirror neuron theory makes at least three strong claims about the character of the shared mechanism of action production and action understanding, which distinguish it from cognitive, nonembodied theories.

First, the core, novel claim of the mirror neuron theory concerns the motor nature of the representations carried by mirror neurons. The idea that the motor system is involved not only in movement generation but also in understanding actions and intentions is radically different from classical theories for which these processes require the involvement of abstract (or amodal/symbolic) representations.

Second, action understanding mediated by the mirror neuron mechanism is assumed to be direct in the sense that it can be achieved without needing "inferential processing" or other "high-level mental processes" (Rizzolatti & Sinigaglia 2010). The mapping of sensory inputs onto corresponding representations of actions within the motor system is thus postulated to be largely automatic. It presumably does not account for factors such as prior beliefs, specifics of the situation, or the context in which an observed action is carried out because all these likely require the "high-level mental processes" that direct matching between an observed action and a motor representation circumvents. Instead, the matching depends on a "natural response" of the mirror system to the visual input (Rizzolatti & Sinigaglia 2010; but see Cook et al. 2014).

Finally, action understanding involves simulation of the observed actions in the motor system of the observer: Whenever an individual observes an action, his or her understanding is mediated by the same population of premotor neurons that also control his or her own execution of that action. The relevant action is effectively reenacted within the observer's premotor cortex (Rizzolatti & Sinigaglia 2010).

Basic Properties of Macaque Mirror Neurons

Early on after the discovery of mirror neurons, many studies focused on characterizing their basic response properties. At least three important findings emerged from these investigations.

Mirror neurons are activated only by particular kinds of actions. Mirror neurons fire only when the monkey is presented with a natural, transitive action that targets a simultaneously presented object (di Pellegrino et al. 1992), for instance, when the experimenter grasps a piece of food in front of the monkey. Mirror neurons would not fire when the experimenter only moves his hand toward the food but does not grasp it. Furthermore, they would not fire during the presentation of the food alone or when the experimenter performs a grasping movement in absence of an object. Thus, mirror neuron activity during visual observation appears to be triggered by object-directed actions (but see Kraskov et al. 2009).

Mirror neurons have different degrees of congruency. The actions that cause the mirror neuron to fire during both motor production and action observation tend to be congruent

(Gallese et al. 1996). For instance, a mirror neuron that is active when the monkey grasps an object with a precision grip is likely to be activated when the monkey observes the same or a similar action. However, the degree of congruency varies considerably across different mirror neurons. Some mirror neurons exhibit a strict relationship between the performed and observed actions that activate them, such as grasping with a specific type of grip, whereas others fire even when the relationship between the observed and performed action is very loose, such as neurons that respond when an action is performed but are activated by the sight of multiple different actions. Finally, for some mirror neurons there is no clear relationship between observed and performed actions.

Mirror neurons are sensitive to the goal of an action. The observations of congruence between the observed and the executed actions triggering some of the mirror neurons led investigators to propose that mirror neuron activity correlates with action understanding (di Pellegrino et al. 1992, Gallese et al. 1996, Rizzolatti et al. 1996). One of the most influential studies cited in support of such claims is an experiment by Umiltà et al. (2001). In the experiment, two monkeys viewed hand actions performed by an experimenter such as grasping, holding, or placing in two conditions. In one of the conditions, the monkeys observed the actions from start to finish without interruption. In the other condition, the monkeys could only observe the initial stage of the action, but the final stage, during which the hand interacted with the object, was occluded. The researchers found that some neurons in area F5, which showed mirror properties when the monkeys observed the entire hand action sequence, also responded when the final stage of the action was occluded. The authors interpreted this result to mean that, on the basis of the observed part of the action sequence, the monkey understood the action being performed; thus, its understanding was reflected in the activity of the mirror neurons. Because the monkey typically understands the action before it is completed, the firing of these mirror neurons is sustained even if the final part of the action is occluded. Therefore, mirror neuron activity correlates with action understanding.

A study by Fogassi et al. (2005) provided another piece of evidence supporting the correlation between mirror neuron activity and action understanding. The authors recorded neurons in the convexity of the inferior parietal lobule (IPL) of a monkey that responded selectively to reaching actions with extremely similar motor profiles: either reaching for a piece of food and placing it in its mouth or reaching for a piece of food and placing it in a container affixed close to its head. Some of these neurons retained their selectivity for one specific type of action when the monkey was passively viewing the experimenter's actions. Fogassi et al. (2005) take these findings to indicate that the mirror neurons in question selectively encode goals of motor acts and thus facilitate action understanding. They also suggest that intentions are understood by activating one of several possible motor chains (e.g., grasp-to-place versus grasp-to-eat).

The experiments by Umiltà and colleagues (2001) and by Fogassi and colleagues (2005) provide clear cases of mirror neuron activity being sensitive to fairly subtle distinctions between different kinds of observed actions. However, whether these neurons actively contribute to action understanding or whether their activity is only correlated with it is not directly addressed by these experiments. That is, they do not rule out the possibility that mirror neuron activity results from processes that occur in other parts of the brain that mediate action understanding. When a monkey observes an action whose final part is occluded (as in Umiltà et al. 2001), assuming the monkey correctly infers the kind of action being performed, at least two accounts of the mirror neuron activity pattern are equally plausible. On the one hand, the mirror neurons could be actively contributing to the categorization of the observed action. On the other hand, the action could be categorized outside the motor system, and a corresponding nonmotor representation of the action (e.g., crack a nut to get food) could be retrieved (Mahon & Caramazza 2008).

Properties of the Human Mirror System

In the human brain, studies show that the inferior limb of the precentral sulcus/posterior part of the inferior frontal gyrus, the inferior parietal lobe, and the superior temporal sulcus, and recently also the supplementary motor cortex, the primary somatosensory cortex, and visual area MT are recruited during both observation and imitation/execution of actions (Chong et al. 2008, Dinstein et al. 2007, Grèzes et al. 2003, Iacoboni et al. 1999, Kilner et al. 2009, Press et al. 2012; for a recent meta-analysis, see Caspers et al. 2010). Using TMS, many studies have demonstrated that action observation leads to highly effector-specific and even muscle-specific modulations of corticospinal excitability (e.g., Cattaneo et al. 2009, Fadiga et al. 1995, Maeda et al. 2002, Urgesi et al. 2010).

Using multi-voxel pattern analysis (MVPA), Oosterhof et al. (2010) observed above-chance classification of actions across modalities in the left postcentral gyrus and the left anterior parietal cortex. Using a similar approach, Oosterhof et al. (2012) found that the parietal and occipitotemporal cortices contained cross-modal action-specific representations irrespective of the viewpoint of the observed action. By contrast, the ventral premotor cortex contained action-specific representations across modalities for the first- but not the third-person perspective (Caggiano et al. 2011, Maeda et al. 2002). These studies show that high-level representations of actions are not restricted to early sensorimotor areas (but see Cattaneo et al. 2010). Despite various methodological advances, the types of content represented in the various regions of the human mirror system and whether these contents are specifically motor or more abstract remain unclear (Dinstein et al. 2008, Hickok 2009, Oosterhof et al. 2013).

Direct Matching and Simulation

The proposal that conceptual understanding is achieved through sensorimotor simulation is integral to embodied theories of cognition, and in the context of the mirror neuron theory of action understanding, it is intimately linked with the notion of direct matching. On this theory, direct matching is a mechanism through which sensory inputs associated with actions of other individuals are mapped unmediatedly, without involving "higher-level mental processes" such as "inferential processing," onto motor representations in the observer's brain (Rizzolatti & Sinigaglia 2010).

Data from numerous experiments have been interpreted to support the claims of direct matching in action understanding (see especially Fogassi et al. 2005, Gallese et al. 1996, Kohler et al. 2002, Rizzolatti et al. 1996, Umiltà et al. 2001). In one of the most widely cited studies, Kohler and colleagues (2002) report finding mirror neurons in the macaque monkey that become active both when the animal visually observes an action and when it hears a sound that is associated with that action. For example, in one experimental condition, some neurons became active when the monkey cracked a peanut, when visually observing the experimenter crack a peanut, and when hearing the sound of the action alone. The authors interpret these observations as evidence supporting the direct matching hypothesis.

Such an interpretation raises an important question about the nature of the link between incoming sensory representations and the subsequently retrieved motor representations. Mapping the sound of an action onto the motor program corresponding to it requires relatively rich prior knowledge about the action. In the case of visual observation, one could establish a correspondence between the low-level visual inputs and motor representations in the premotor cortex. The information about an action contained in the visual signal allows one to determine which effectors were used and what their position and speed were, among other properties of the action. In contrast, the auditory signal alone provides much less information to establish a correspondence with a motor representation of an action; for example, the sound does not carry information about the effector involved in the action. The triggering of mirror neurons by action sounds represents a learned association that could, in principle, be established between an arbitrary sound and an arbitrary motor representation. The fact that the motor representation of the correct action has been retrieved in the motor system even though the sensory signal alone does not contain sufficient information to determine which motor action was performed implies that the action has already been categorized by the time the motor system is activated. It is not obvious how to reconcile the data about auditory triggering of mirror neurons with the direct matching hypothesis.

ARE MIRROR NEURONS MOTOR?

The centrality of motor representations in action understanding—the claim that mirror neurons are essentially motor—is the defining characteristic of the mirror neuron theory. However, the sense in which mirror neurons can be considered motor, what evidence supports such a claim, and its implications for embodied theories of action understanding are not clear.

Mirror neurons can be considered motor in several ways. First, and most straightforward, is that these neurons fire during active movements, and their responses are selective, responding during certain movements and not others (di Pellegrino et al. 1992, Rizzolatti et al. 1996). However, by definition, mirror neurons are also activated during action observation. Therefore, in this sense, the representations carried by mirror neurons are also visual, and one cannot conclude that actions are understood by reenacting motor representations without also concluding that actions are executed by reenacting visual representations. Thus, the visuomotor character of these neurons does not favor choosing one modality over the other.

A second sense in which the representations carried by mirror neurons are motor is that these neurons were found in areas of the brain that are historically considered motor. Rizzolatti & Sinigaglia (2010) seem to argue that the motor function of mirror neurons depends on their anatomical location. Neurons in area F5, where mirror neurons were found originally (di Pellegrino et al. 1992, Gallese et al. 1996, Rizzolatti et al. 1996), respond during action execution (Kurata & Tanji 1986, Rizzolatti et al. 1981). Thus, mirror neurons could then be considered motor. However, mirror neurons, by definition, also respond to visual stimuli. Area F5 also contains mirror-like neurons that do not fire during action execution and fire only during action observation (di Pellegrino et al. 1992; Gallese et al. 1996, 2002). Accepting the assumption above would lead to the conclusion that even these mirror-like neurons are motor, despite that they are not activated at all during action execution.

In what sense, then, could mirror neuron representations be motor in a way that justifies an embodied theory of action understanding? The motor modality may be predominant over the visual modality in mirror neuron representations in the sense that the informational content of the representations carried by mirror neurons specifies details that are particularly relevant for motor execution (e.g., which muscles are used to perform an action) but not for visual processing (e.g., where they are presented in the visual field). In this case, mirror neurons may be considered predominantly motor in the sense that they carry details specific to the motor modality, but they do not carry other details specific to the visual modality. This determination would allow investigators to interpret mirror neuron activation in terms of reenacting specific motor programs.

A study by Umiltà et al. (2008) is relevant to this issue. These authors investigated the response properties of neurons in areas F5 and F1 of the premotor cortex of monkeys after they were trained to use normal pliers, which require a squeeze action to hold an object, and inverse pliers, which require a squeeze action to release an object. The response pattern of most of the F5 and some of the F1 neurons when monkeys grasped with pliers was extremely similar to the response these neurons exhibited when monkeys grasped objects with reverse pliers. These data thus shed light on how specific the representations mediated by the F5 and a portion of the F1 neurons actually are. The data suggest that neuron activity reflects abstract action properties, such as outcome, rather than just the sequence of motor programs that need to be executed in order to obtain that outcome.

The neurons studied by Umiltà et al. (2008) were not mirror neurons. However, the authors hypothesize that because mirror neurons are found in the same brain regions as those studied in the experiment, one would expect at least some mirror neurons to exhibit the same degree of generalization across different motor actions with the same overall goal. Consistent with this view, Gallese and colleagues (1996) report finding mirror neurons that fire during observation of grasping performed by a monkey either with the hand or with the mouth, a clear indication that mirror neurons represent abstract action goals as opposed to specific motor contents.

Thus far we have adopted a simplified distinction between low-level motor representations and higher-level (abstract, cognitive) representations previously employed in the mirror neuron literature (Rizzolatti & Sinigaglia 2010). Although this distinction can be helpful as a first approximation, it remains unclear on the basis of which criteria the boundary should be drawn. The empirical findings indicate that a richer view is required to appropriately describe the wealth of evidence available in the literature. Action observation and understanding seem to be the outcomes of numerous processing stages at different levels, from early visual areas to the superior temporal sulcus (STS) to the mirror system in the inferior parietal lobe and F5, etc. In a recent study, Mukamel et al. (2010) reported that neurons in the human medial temporal lobe, including the hippocampus and the amygdala, fired both during the execution and the observation of similar actions. These findings indicate that representations active during action execution and action observation are also present outside the regions historically considered motor. The human medial temporal lobe is a highly multimodal brain area known to contain neurons that carry high-level representations of objects that generalize beyond specific views (Kreiman et al. 2000, Quiroga et al. 2005), supporting the hypothesis that these cells store the meaning of a stimulus.

SUMMARY AND CONCLUSIONS

We have provided an overview of the most important empirical results concerning embodied cognition theories and have presented a partial assessment of them, as well. Research motivated by embodied accounts of cognition led to the discovery of many phenomena supporting the close interaction between conceptual processing and sensorimotor representations.

In the context of embodied cognition theories, this body of extraordinarily interesting empirical data has been used by some investigators to argue that conceptual knowledge is mediated primarily by sensorimotor representations and that sensorimotor simulation is an essential part of conceptual processing. We have shown that these claims are unwarranted for two main reasons. First, a substantial part of the evidence cited in support of embodied cognition theories concerns phenomena for which the predictions of embodied and cognitive theories coincide. Therefore, such evidence does not discriminate between embodied and cognitive accounts. In fact, every cognitive theory assumes that perception and action, comprehension and production are bridged through shared, abstract conceptual representations. Cognitive theories would suffer from a strange duality of the mind if there were no possibility for an exchange among perception, action, and conceptual processing. Second, in the field of action understanding, studies on mirror neurons have shown that areas that were thought to carry relatively low-level representations contain neurons that show surprisingly high levels of abstraction (Caggiano et al. 2011, 2012; Ferrari et al. 2005; Gallese et al. 1996; Umiltà et al. 2001, 2008) that, we argue, cannot plausibly be considered motor. At the same time, single-cell recordings in humans individuated neurons located outside the so-called motor system that represent actions with perhaps even greater abstraction (Mukamel et al. 2010). These results suggest that conceptual processing relies on high-level, nonsensorimotor, abstract representations.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

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