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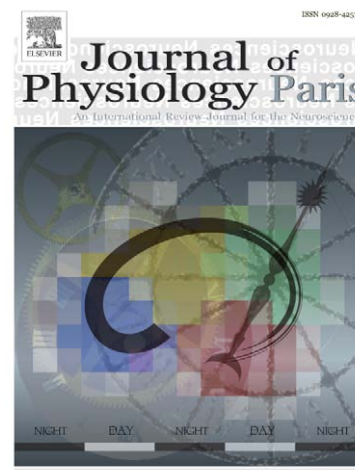
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Embodied semantics for actions: Findings from functional brain imaging

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Abstract

The theory of embodied semantics for actions specifies that the sensory-motor areas used for producing an action are also used for the conceptual representation of the same action. Here we review the functional imaging literature that has explored this theory and consider both supporting as well as challenging fMRI findings. In particular we address the representation of actions and concepts as well as literal and metaphorical phrases in the premotor cortex.

Keywords: embodied semantics, representation of actions, literal and metaphorical phrases.

1. Introduction

The theory of embodied semantics states that concepts are represented in the brain within the same sensory-motor circuitry in which the enactment of that concept relies. For example, the concept of “grasping” would be represented in sensory-motor areas that represent grasping actions; the concept of “kicking” would be represented by sensory-motor areas that control kicking actions; and so forth. This theory indicates that the secondary sensory-motor areas, which are known to be involved in mental simulation of world experiences (Rizzolatti & Craighero, 2004), may be responsible for the representation of concepts (Gallese & Lakoff, 2005). Instead, primary sensory-motor areas are presumed to be inhibited, in order to distinguish between a general representation of a given concept and its actualization. This theory has been extended by Lakoff and his colleagues to include metaphors. Thus the phrase “kick off the year” would also involve the motor representations related to kicking, just as the phrase “grasp the explanation” would involve motor representations related to control of the hand (Lakoff & Johnson, 1999). Ideas along similar lines have been discussed previously by other groups (for example, Barsalou, 1999; Damasio, 1989; Damasio & Tranel, 1993; Feldman & Narayanan, 2004; Glenberg & Kaschak, 2002; Pulvermuller, 2005; Pulvermuller, Hauk, Nikulin, & Ilmoniemi, 2005).

While embodied semantics would apply to all concepts, (i.e., concepts associated with visual movement would be represented by visual motion areas such as MT, etc), most efforts to date have been placed on investigating the neural correlates of concepts

associated with actions (kicking, grasping, biting, etc.). Here we review first some neuropsychological literature investigating the link between language and motor processing, then move to the link between embodied semantics for language and the mirror neuron system and fMRI data on embodied semantics for actions. Next we consider representations for language and for actions in BA 44, and finally embodied semantics for metaphors.

2. Neuropsychological studies on motor and action verb processing

The lesion method has proven to be a powerful tool for assessing processing of actions by motor areas. Specifically, embodied semantics for actions, as commonly stated, would lead one to expect that damage to premotor cortex would produce impairments in action comprehension. This question has been asked in a number of neuropsychological studies, with inconclusive results. Heilman and his colleagues tested patients with apraxia due to left hemisphere lesions on various tasks involving action comprehension. The patients were divided into two groups, those with posterior lesions and those with anterior lesions. The latter would likely include premotor cortex, although there was no detailed reports of the neuropathology. While the two groups were pre-selected to be similarly affected on motor tasks, only the patients with posterior lesions were impaired on the action comprehension tests (Heilman, Rothi, & Valenstein, 1982; Rothi, Heilman, & Watson, 1985). These results are consistent with the traditional model of praxis proposed by Liepmann (reviewed in Leiguarda & Marsden, 2000) in which the left parietal lobe supports common representations for action production and

comprehension (see also De Renzi, Faglioni, Scarpa, & Crisi, 1986; Kertesz & Ferro, 1984).

However, several studies have shown that action comprehension may be compromised in patients with damage to frontal premotor areas. In particular, the overlap for cognition and motor processing was found in motor neuron disease (MND), a neurodegenerative disease selectively affecting the motor system (Bak & Hodges, 1999, 2004; Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001). Action verb production and comprehension, as compared to processing of nouns, appear to be significantly compromised in patients with MND. Post-mortem examination of affected MND patients revealed damage to the motor and premotor cortex, including pathology in the inferior frontal gyrus (Brodmann areas 44 and 45), indicating that these areas are not only essential for motor processing, but also for processing of action verbs (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001). Examinations of patients with progressive supranuclear palsy (PSP) (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994) and frontotemporal dementia (Cappa et al., 1998) further support the notion that a deficit in verb processing may be associated with damage to frontal and frontostriatal brain areas.

Furthermore, Tranel et al. investigated the conceptual representation for actions in 90 patients with lesions to various sites in the left or right hemisphere. The retrieval of knowledge for actions was measured by asking participants to evaluate action attributes from viewing pictures of actions and compare and match pictured actions. Using a lesion overlap approach, they reported that the highest incidence of impairment was correlated

with damage to left premotor/prefrontal cortex, the left parietal region, and the white matter underneath the left posterior middle temporal region (Tranel, Kemmerer, Damasio, Adolphs, & Damasio, 2003). A similar dual-pattern of deficit was reported in a study in which aphasic patients were tested for their comprehension of visually or verbally presented actions: patients with lesions of premotor or parietal areas were impaired on these tasks, although lesions in premotor areas were more predictive of deficits (Saygin, Wilson, Dronkers, & Bates, 2004).

Taken together, these studies indicate that action comprehension deficits can be observed in patients with premotor lesions. The fact that similar deficits are found in patients with parietal lesions (and that there are other reports in which patients with anterior lesions performed normally (see Schnider, Hanlon, Alexander, & Benson, 1997; Wang & Goodglass, 1992), makes it hard to draw definitive conclusions from this work. It should be noted that even if it was found that processing in the premotor cortex was essential for action comprehension, the theory of embodied semantics would not be refuted. The focus would instead shift to other regions which are commonly active for action production and comprehension, such as the parietal cortex (Fogassi et al., 2005).

3. Relation of Embodied Semantics to the Mirror Neuron System

Recently, the discovery of mirror neurons has prompted a series of functional imaging studies investigating embodied semantics for actions. Mirror neurons, first discovered in area F5 of the monkey brain, are activated both during action execution and action observation (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese,

Fadiga, Fogassi, & Rizzolatti, 1996), during the mental simulation of the action (Umiltà et al., 2001), and when the sound associated with an action is perceived (Kohler et al., 2002). Furthermore, neurons in the mirror system are most sensitive to the goal of the action regardless of the specifics of how the action is performed (for example, the use of the hand or the foot, the exact affordances, etc). Thus one group of neurons may be sensitive to “grasping” in general, while another group to “tearing”, and this generalized abstraction expands across the different affordances and effectors used (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). This generalization of an action is thought to be essential for the formulation of a concept (Gallese & Lakoff, 2005).

There is now evidence from several studies that the mirror system is also present in humans in BA 44, which is thought to be the human homologue of monkey F5 (Geyer, Matelli, Luppino, & Zilles, 2000), as well as more dorsal sectors of the premotor cortex, and in the inferior parietal lobule (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006; Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gazzola, Aziz-Zadeh, & Keysers, 2006; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 1999; Nishitani & Hari, 2000). Thus the finding of a mirror system equivalent in humans strengthens the biological plausibility of the embodiment of action concepts.

How might such a mirror system work? One possibility is that, in repeated instances of learning, signals related to the representations of actions in primary and

secondary motor and sensory areas are relayed by feed-forward convergent projections to the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL). From many distributed sources, the signals converge into a few sites and these resulting “convergence zones” naturally interrelate visual, somatosensory (kinesthetic), and motor information (Damasio, 1989). For example, a number of neurons representing varieties of “grasping” actions in the primary and pre- motor cortex (precision grip, whole hand prehension, etc.), as well as neurons in STS and the auditory cortices representing visual and auditory events which co-occur with these actions, would all relay convergent information on “grasping” to groups of neurons in the IFG/IPL. The feed-forward signals from the feeding cortices are conjoined by temporal coincidence (for signals that co-occur) and temporal sequencing of activation (for signals involved in representing sequences of actions). The consequences of this arrangement is that the converged upon neurons, by virtue of learning, code for the set of sensorimotor events associated with an action, such as “grasping”. Subsequently, the reprocessing of signals that were part of the original set, for example, visual signals, prompts the reprocessing of somatomotor and auditory components of the same set via divergent back projections. Likewise, reprocessing of somatomotor components of a set entails the reactivation of visual or auditory components of that set. The signals related to the common goal for a variety of specific actions, i.e., grasping with the mouth, or with the hand or toes, along with related affordances, could also converge on a particular group of neurons thus providing a more general representation of “grasping”. This would be the basis for generalized conceptual representations, which could be then related to language descriptors. [Ideas discussed by

Pulvermuller and Rogers are compatible with this view (Pulvermuller, 1999; Rogers et al., 2004).]

This kind of circuit architecture, imbued with learning properties, would be a precondition for the appearance of neurons with mirror properties. Another precondition would be the comprehensive representation of the structure and operation of the varied aspects of the subject's own body in the subject's own brain (in somatomotor regions including the somatosensory association cortices, the premotor cortices, and the insular cortices). Such a "self" representation would be the basis for "as if" simulations, and would permit the correspondence between actions seen in others and the subject's own simulated actions (Damasio, 1994; Damasio & Damasio, 2006).

4. Embodied Action Semantics in the Premotor Cortex using fMRI

Several studies have found support for embodied action semantics in the premotor cortex using fMRI. In a study by Hauk and his colleagues, it was found that reading words associated with foot, hand, or mouth actions (e.g., kick, pick, lick) activated motor areas adjacent or overlapping with areas activated by making actions with the foot, hand, or mouth (Hauk, Johnsrude, & Pulvermuller, 2004). Tettamanti and his colleagues also found that listening to action related sentences activated the premotor cortex in a somatotopic fashion; leg sentences showed premotor activity dorsal to hand sentences dorsal to mouth sentences (Tettamanti et al., 2005). In another study, Aziz-Zadeh and colleagues (2006) localized foot, hand, and mouth premotor regions of interest in each subject by having them watch actions with each effector, and also read phrases associated

with the foot, hand, or mouth. They found that in each subject, the regions most activated for watching a foot action were also most active for language related to foot actions. The same was true for the hand and the mouth (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006).

While these findings generally support embodied action semantics, it should be noted that there is a great deal of variance among the specifics in each study. In particular, a substantial amount of variability in peak coordinates has been reported for somatotopic responses to action observation and linguistic stimuli (Buccino et al., 2001; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). In a study by Aziz-Zadeh and colleagues, bilateral premotor activations for observing the mouth versus rest, and a left-lateralized activation for observing the hand versus rest were found. The mouth region was ventral to the hand area, in line with the well-known arrangement of the motor homunculus (Penfield & Rasmussen, 1950) as well as with previous studies of action observation (Buccino et al., 2001; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). The regions found for action observation are reasonably close to some reported peak locations but not others. The dorsal hand activation peaked at $(-30, -6, 46)$, which is 26 mm from the closest location of $(-56, -4, 44)$ reported by Buccino et al. (2001); in fact the region Aziz-Zadeh et al. found is much closer to a hand language peak reported by Tettamanti et al. (2005): it is 11 mm away from their peak of $(-30, -2, 56)$. The left hemisphere mouth peak we found at $(-54, 4, 26)$ is 17 mm from the closest peak reported by Buccino et al. (2001): $(-64, 12, 20)$, and again is closer to activations reported for

language: 10 mm from the peak of (-44, 2, 24) reported by Tettamanti et al. (2005), and 9 mm from the peak of (-50, 10, 20) reported by Hauk et al. (2004) (See Figure 1).

The different contrasts used in the different studies may be responsible for some of the variance among the findings, but it is noteworthy that two studies of premotor activations for action *execution* have failed to distinguish between peaks activated for the hand and the foot (Fink et al., 1997; Kollias et al., 2001). Thus the degree of somatotopic organization of premotor cortex in humans remains poorly understood. Aziz-Zadeh et al. did not note any area to be differentially activated by observation of the foot, unlike Buccino et al. (2001) and Wheaton et al. (2004) who did. It is well known that the hand and the mouth are over-represented in the motor homunculus, whereas representations for the foot are significantly smaller. This might be one reason why Aziz-Zadeh et al. observed effector-specific activations for the hand and the mouth only, but not for the foot.

Another consideration with regards to the organization of premotor cortex, especially in the context of embodied semantics, is that somatotopy may be only one of several general organizing principles. During action observation, Aziz-Zadeh et al. found only the mouth to be ventral to the hand (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006). This limited somatotopy may be a reflection of organization by effector, the goal of the action, medial versus proximal distinctions, and so forth (Schubotz, von Cramon, & Lohmann, 2003; Schubotz & von Cramon, 2003; Sakreida et al., 2005). Indeed, the hand versus mouth somatotopy found here could also be classified as a distinction between

reaching (the reach and grasp of the arm) and operating upon (biting with the apple). It is interesting to note that activation during foot observation, which did not reach the minimum cluster size, occurred ventrally, overlapping the mouth activation. This is a possible indication that foot actions were interpreted as “operating upon” actions, like the mouth actions, as opposed to the reaching actions of the hand. In fact, Rizzolatti and colleagues have suggested that action plan (e.g. manipulating, reaching) is more important than the actual effector involved (Rizzolatti et al., 1987). Future studies should distinguish among these alternatives, especially before specific conceptual representations are tied to specific premotor areas.

5. Embodied Action Semantics in BA 44

How are action and language represented in BA 44? Aziz-Zadeh et al (2006) found that although both action observation and reading phrases about actions caused activity in premotor and prefrontal regions in the vicinity of Broca’s area, the activated regions largely did not overlap. Activations for reading phrases were anterior and medial to activations for action observation. This result contrasts with that of Hamzei et al. (2003) who stressed the overlap of language and action observation activations in the inferior frontal gyrus. Hamzei et al. however used a verb generation task that evoked widespread activation in the inferior frontal gyrus and the premotor cortex, and their action observation task led to a relatively small area of activation within this larger area, hence the overlap. The reading task used by Aziz-Zadeh et al. produced much less extensive frontal activations, allowing areas activated by reading and by action observation to be clearly distinguished (Figure 2). It is also interesting to note that Hamzei and colleagues

typically observed different peaks for action observation and language in individual subjects, however these pairs of peaks did not bear any consistent spatial relationship to one another. This finding, along with the results from Aziz-Zadeh et al 2006, suggests that although mirror neurons in Broca's area may be a crucial precursor for the development of language (Rizzolatti & Arbib, 1998), future theoretical work developing this account should consider the fact that the brain areas involved in the two systems are not identical. However, a developmental account proposed before the first report on mirror neurons (Greenfield, 1991), suggested a trajectory which may recapitulate the evolutionary trajectory: early on in development, neural resources for action and language are shared, but later on they differentiate into adjacent, but separate neural systems. Thus, as Iacoboni has pointed out, it is critical to consider that the study by Aziz-Zadeh et al. studied adult subjects and that future developmental work in young children may reveal a different pattern of neural organization for action and language (Iacoboni, personal communication).

6. Metaphorical Language

Do metaphorical uses of words associated with the hand, foot or the mouth activate motor areas? Aziz-Zadeh et al. (2006) considered this possibility in an action observation and language study, by considering metaphors related to actions (e.g, "bite the bullet", "grasp the meaning", "kick the bucket.") (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006). Subjects read these phrases and also observed videos of hand, foot, and mouth actions, and the experimenters looked for correspondences between language and action for each effector. Evidence for congruent somatotopic organization of semantic

representations for metaphorical sentences in either hemisphere was not found. It is important to note, however, that the metaphors used in the study are over-practiced. It is possible that once a metaphor becomes well established, it no longer activates the same network of processing that it may have initially. When first encountered, a metaphor like “grasping the situation” may have used hand representations in order to be understood. However, once it is properly learned it may no longer rely on these representations and may use, instead, other representations having to do with the concept of “understanding”. This hypothesis could be tested by investigating activations to metaphors on a continuum, from novel to over-learned, with the prediction that novel metaphors would more strongly activate sensory-motor representations than over-learned metaphors.

Indeed, recent studies have explored differences between novel and conventional metaphors. The results indicate that distinct brain areas may subservise processing for each type of metaphor (Bottini et al., 1994; Mashal, Faust, Hendler, & Jung-Beeman, 2007; Schmidt, DeBuse, & Seger, 2007). In general, these studies distinguish only between novel and conventional metaphors and do not consider types of metaphors within each category (e.g. actions, etc.), which would test the embodied semantics hypothesis. However, they do indicate that different brain areas process the two kinds of metaphors, with the right hemisphere specifically more active for novel metaphor processing. This finding has been related to the Graded Salience Hypothesis (GSH) (Giora, 1997, 1999; Mashal, Faust, Hendler, & Jung-Beeman, 2007). GSH predicts that salient meanings are accessed more quickly than less salient meanings. Thus highly familiar meanings that are represented in the mental lexicon are accessed more readily. According to this model,

conventional metaphors, such as “grasp the situation”, the metaphorical meaning (to understand) is more salient than the literal meaning (a grasping action). Thus it is the figurative meaning that would be activated first, without needing to access the less salient literal meaning (Gibbs, 1980; Giora & Fein, 1999a, 1999b). Because the metaphorical meaning of novel metaphors are not salient – that is, they are not yet stored in the mental lexicon – these representations would not be activated first. Instead, for novel metaphors, the literal meaning would be more salient and accessed most readily. In brief, this theory supports the prediction that novel metaphors could be processed using embodied literal representations whereas conventional overlearned metaphors would instead use the more salient intended meaning of the metaphor.

7. Conclusions

It was the aim of this paper to discuss not only the fMRI findings related to embodied semantics for actions, but also to consider some challenges this research program will need to consider in the future. Understanding representations in the premotor cortex will be necessary to understand better how conceptual representations may arise. Furthermore, exploring the link between these conceptual representations and metaphorical language is especially important, as it has been proposed that much of abstract thinking is performed metaphorically (Lakoff & Johnson, 1999). Finally, linking the action system to language and perceptual areas in the brain will be essential for a more complete model of embodied semantics. To this end, imaging methods with good temporal resolution (EEG/MEG) and functional connectivity analyses will also be

important for revealing the sequence of activation patterns involved in embodied semantic processing.

ACCEPTED MANUSCRIPT

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Figure Captions

Figure 1: Activation of premotor cortex activity for execution (squares), observation (circles), and language (triangles) related to the foot (red), hand (green), or mouth (blue) plotted in MNI coordinates. Execution coordinates are taken from reports by Finke et al. (1997) and Koliass et al. (2001). Action observation coordinates are taken from reports by Buccino et al. (2001), Wheaton et al. (2004), and Aziz-Zadeh et al. (2006b). Language coordinates are taken from reports by Hauk et al (2004), Tettamanti et al. (2005), and Aziz-Zadeh et al. (2006b).

Figure 2: Activation for action observation of the foot, hand, or mouth (red) and reading phrases related to the foot, hand, or mouth (blue). Of particular interest are the activity patterns for both in the vicinity of Broca's Area in the upper left (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006).

