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Semantic domain-specific functional integration for action-related vs. abstract concepts

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ABSTRACT

A central topic in cognitive neuroscience concerns the representation of concepts and the specific neural mechanisms that mediate conceptual knowledge. Recently proposed modal theories assert that concepts are grounded on the integration of multimodal, distributed representations. The aim of the present work is to complement the available neuropsychological and neuroimaging evidence suggesting partially segregated anatomo-functional correlates for concrete vs. abstract concepts, by directly testing the semantic domain-specific patterns of functional integration between language and modal semantic brain regions. We report evidence from a functional magnetic resonance imaging study, in which healthy participants listened to sentences with either an action-related (actions involving physical entities) or an abstract (no physical entities involved) content. We measured functional integration using dynamic causal modeling, and found that the left superior temporal gyrus was more strongly connected: (1) for action-related vs. abstract sentences, with the left-hemispheric action representation system, including sensorimotor areas; (2) for abstract vs. action-related sentences, with left infero-ventral frontal, temporal, and retrosplenial cingulate areas. A selective directionality effect was observed, with causal modulatory effects exerted by perisylvian language regions on peripheral modal areas, and not vice versa. The observed condition-specific modulatory effects are consistent with embodied and situated language processing theories, and indicate that linguistic areas promote a semantic content-specific reactivation of modal simulations by top-down mechanisms.

1. Introduction

The debate on the nature of concepts has been feeding philosophic discussion for centuries, mainly focusing on the ontological status of concepts and on the well-known referential problem. In cognitive neuroscience, in turn, the debate hinges on the specific structure, format, and content of concepts. Two main types of theories about conceptual knowledge have been proposed. The so called amodal theories claim that knowledge is represented in semantic memory by amodal and arbitrary symbols governed by syntactic combinatorial rules (e.g., Fodor, 1975; Newell & Simons, 1972; Pylyshyn, 1984). According to this view, all concepts are symbolic and abstract and are represented in systems separated from the modal neural systems underlying perception and action. However, there is little empirical evidence supporting amodal theories (Machery, 2007). An unresolved challenge for this type of hypothesis is specifying where amodal symbols are stored in the brain and whether the proposed neural representations are compatible with neural principles of computation (Barsalou, 1999, 2008; Pulvermueller, 1999). An alternative point of view is represented by modal theories asserting that concepts are grounded on multiple, distributed representations. Some of these theories focus on simulation, such as the perceptual symbol system proposed by Barsalou (1999); others focus on situated action (Glenberg & Kaschak, 2002; Glenberg & Robertson, 2000) or on bodily states (Gallese, 2007; Gallese & Lakoff 2005). Within modal theories, concepts are interpreted as the mental simulation of specific things or events, i.e., implicit and automatic concept-driven reactivations of the very same schematic simulations engaged during primary processes (Barsalou, 1999, 2008; Barsalou, Kyle Simmons, Barbey, & Wilson, 2003). Evidence from neuropsychology and functional neuroimaging show that information about the relevant features of an object—such as visual, auditory, and olfactory, the manner

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in which it moves, and its name—is partially stored in the same sensory and motor systems activated during the acquisition of that information (Boronat et al., 2005; Gainotti, 2004; Gonzalez et al., 2006; Martin, 2007; Patterson, Nestor, & Rogers, 2007; Perani et al., 1995; Simmons, Martin, & Barsalou, 2005).

At a purely theoretical level, a theory about conceptual knowledge can only be considered valid if it is able to account for the processing of virtually any kind of concepts. An important implication of modal theories is that they take into account both concrete and abstract concepts, and therefore possess a degree of explanatory power comparable to amodal theories. Perceptual and motor simulations are thought to mainly mediate the representation of concrete concepts. Abstract concepts are thought to be mainly represented via simulation of internal states and/or simulation of factual and contextual situations (Barsalou, 1999, 2008; Barsalou & Wiemer-Hastings, 2005). Here we propose to test modal vs. amodal theories by using the concrete vs. abstract distinction as a paradigmatic model in the language domain.

Convergent evidence from behavioral, physiological and neuroimaging studies have demonstrated the role of perceptual simulations (Gonzalez et al., 2006; Kaschak, Zwaan, Aveyard, & Yaxley, 2006; Kaschak et al., 2005; Meteyard, Bahrami, & Vigliocco, 2007; Pulvermueller & Hauk, 2006) and of motor simulations (see Pulvermueller (2005) for a review) in processing the concrete content of linguistic utterances. For example, Tettamanti and colleagues (2005) showed in a fMRI study that listening to sentences describing actions performed with different body parts (mouth, hand, or leg) activates a left fronto-parieto-temporal circuit with somatotopic organization in the premotor cortex. This evidence, together with results obtained in similar experiments on action words (Hauk, Johnsrude, & Pulvermueller, 2004) and action-related phrases (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006), indicates that the somatotopic activation of motor circuits reflects some aspects of linguistic meaning. However, due to its poor temporal resolution, fMRI does not permit to determine whether the processing of action-related items immediately activates motor circuits—during lexical processing—or if these activations are elicited by subsidiary processes, such as imagining the actions verbally described. Neurophysiological techniques with high temporal resolution offer a source of complementary evidence. Early and automatic involvement of motor areas was demonstrated not only for the recognition of action-related sounds (Hauk, Shtyrov, & Pulvermueller, 2006) but also for the processing of action-related words. The results of ERPs experiments on silent reading of face-, hand-, leg-related words, showing category-specific activations at 200 ms after words onset, indicate that the processing of action words immediately triggers the activation of action-related neural networks (Hauk & Pulvermueller, 2004; Pulvermueller, Harle, & Hummel, 2000). Similar results were obtained in an EEG study on action words (Shtyrov, Hauk, & Pulvermueller, 2004) and in a MEG study investigating the time course of cortical activity during action-related word processing (Pulvermueller, Shtyrov, & Ilmoniemi, 2005). Behavioral measures have shown interaction effects between linguistic and motor-perception tasks, supporting the claim that the same mechanisms involved in the perception of events or in action execution are used during the comprehension of language describing the corresponding events or actions. This involvement was interpreted as a necessary requisite to understand language (Boulenger et al., 2006; Buccino et al., 2005; Kaschak et al., 2005; Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008). The results of TMS studies show a specific influence on motor system activity in response to action-related word processing (Buccino et al., 2005; Pulvermueller, Hauk, Nikulin, & Ilmoniemi, 2005). In sum, these results indicate that action simulation is specific, automatic and presents temporal dynamics compatible with its role in language comprehension. These data suggest the existence of shared neural substrates for action and language. A plausible hypothesis is that the mirror-neuron system (premotor and parietal brain regions that respond both to action execution and observation) represents the key neural substrate for action-related language processing (Aziz-Zadeh et al., 2006; Gallese, 2007; Gallese & Lakoff, 2005; Rizzolatti & Craighero, 2004).

While there is a growing body of literature on the neural mechanisms underlying the representation of concrete concepts, there is presently little evidence about the neural mechanisms underlying the perceptual simulation of internal states, such as emotions, and the simulation of factual and contextual information. As proposed by Barsalou (1999, 2008; Barsalou & Wiemer-Hastings, 2005), this type of simulation could provide much of the semantic representations that are central to abstract concepts. Some tentative lines of support to this perspective came from two fMRI studies that investigated the auditory processing of action-related and abstract sentences (Tettamanti et al., 2005, 2008). In the former study (Tettamanti et al., 2005)—discussed above with respect to action-related sentences—sentences with an abstract content, such as "I appreciate sincerity", activated the retrosplenial cingulate cortex. A similar finding was previously reported by Tyler, Russell, Fadili, and Moss (2001). This result was subsequently replicated by a study (Tettamanti et al., 2008), consisting in a factorial combination of concreteness and polarity (i.e., affirmative or negative sentences with either an action-related or an abstract content). The main effect of concreteness, irrespective of the level of polarity, again revealed a higher BOLD signal in the retrosplenial cingulate cortex for the processing of abstract vs. action-related sentences. Advances in the experimental design and in the methods of fMRI data analysis in the second study compared to the first study, allowed us to conclude that the higher BOLD signal in the retrosplenial cingulate cortex for abstract sentences was actually due to a stronger deactivation by action-related than by abstract sentences (Tettamanti et al., 2008). The observation of a relative deactivation in the retrosplenial cingulate cortex prompted a possible interpretation of the findings. The retrosplenial cingulate cortex is a component of the default mode brain system, a system that gathers information about the world around and within us, and that becomes deactivated during goal-directed actions (Greicius & Menon, 2004; Gusnard & Raichle, 2001; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003; Raichle et al., 2001). A relative absence of goal-directed action plans may be associated to abstract vs. action-related sentences, explaining why abstract sentences deactivated the retrosplenial cingulate cortex less than action-related sentences. In addition to its association with introspective/proprioceptive functions, a distinct line of evidence suggests that the retrosplenial cingulate cortex may hold abstract representations of contextual information (Bar & Aminoff, 2003; Canessa et al., 2008; Simmons, Hamann, Harenski, Hu, & Barsalou, 2008). Context representations may be crucial for the simulation of affective and introspective states, as expressed by abstract sentences. In sum, these studies highlighted the importance of the retrosplenial cingulate cortex for the processing of abstract sentences, in relation to introspective state monitoring and contextual representations.

A specific prediction of embodied language theories is that language comprehension is mediated by the fast and automatic cross-talk between speech parsing networks, extracting phonological, morphological, syntactic and semantic information, and modal representations (Barsalou, 1999; Glenberg & Kaschak, 2002). If this view is correct, measures of functional integration (Friston, Harrison, & Penny, 2003; Lee, Friston, & Horwitz, 2006), such as dynamic causal modeling (DCM), should reveal modulations of this cross-talk that are dependent on the semantic content expressed by linguistic utterances. The aim of the present study was to verify this hypothesis, by testing with DCM whether left-hemispheric auditory language processing regions displayed a relatively stronger