Neuropsychologia 50 (2012) 1222–1234

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Reviews and perspectives

A cross-talk between brain-damage patients and infants on action and language

Liuba Papeo[a,b,*], Jean-Remy Hochmann[a]

[a] Department of Psychology, Harvard University, William James Hall, Cambridge, MA 02138, USA
[b] Center for Mind/Brain Sciences, University of Trento, via Belenzani, 12 I-38122 Trento, Italy

ARTICLE INFO

Article history:
Received 23 June 2011
Received in revised form 26 January 2012
Accepted 22 March 2012
Available online 30 March 2012

Keywords:
Word comprehension
Word learning
Sensorimotor processes
Cognitive neuropsychology
Concepts
Aphasia

ABSTRACT

Sensorimotor representations in the brain encode the sensory and motor aspects of one's own bodily activity. It is highly debated whether sensorimotor representations are the core basis for the representation of action-related knowledge and, in particular, action words, such as verbs. In this review, we will address this question by bringing to bear insights from the study of brain-damaged patients exhibiting language disorders and from the study of the mechanisms for language acquisition in infants. Cognitive neuropsychology studies have assessed how damage to representations supporting action production impacts patients' ability to process action-related words. While correlations between verbal and nonverbal (motor) impairments are very common in patients, damage to the representations for action production can leave the ability to understand action-words unaffected; likewise, actions can still be produced successfully in cases of impaired action-word understanding. Studies with infants have evaluated the relevance of sensorimotor information when infants learn to map a novel word onto an action that they are performing or perceiving. These results demonstrate that sensorimotor information is insufficient to fully account for the complexity of verb learning: in this process, infants seem to privilege abstract constructs such as goal, intentionality and causality, as well as syntactic constraints, over the perceptual and motor dimensions of an action. Altogether, the empirical data suggest that, while not crucial for verb learning and understanding, sensorimotor processes can contribute to solving the problem of symbol grounding and/or serve as a primary mechanism in social cognition, to learn about others' goals and intentions. By assessing the relevance of sensorimotor representations in the way action-related words are acquired and represented, we aim to provide a useful set of criteria for testing specific predictions made by different theories of concepts.

Contents

1. Introduction 1223
2. Sensorimotor representations and language understanding 1224
3. What damaged brains tell about the role of sensorimotor representation in action-word understanding 1224
   3.1. Verbs and actions in the left inferior frontal gyrus 1225
   3.2. Associations of language and sensorimotor processes 1225
   3.3. Dissociations between language understanding and sensorimotor processes 1226
4. What learning minds tell about the role of sensorimotor representation in action-word understanding 1227
   4.1. Infants encode observed actions in terms of goals and intentions 1227
   4.2. Conceptual and syntactic constraints on verb learning 1228
5. Discussion 1229
6. Conclusions 1231
   Acknowledgments 1231
   References 1231

* Corresponding author at: Department of Psychology, Harvard University, William James Hall, 33 Kirkland Street, Cambridge, MA 02138, USA.
E-mail addresses: lpapeo@wjh.harvard.edu, liuba.papeo@gmail.com (L. Papeo).

0028-3932/$ – see front matter
http://dx.doi.org/10.1016/j.neuropsychologia.2012.03.025

"*The principal error and the commonest which we may meet with in them, consists in my judging that the ideas which are in me are similar or conformable to the things which are outside me*".
(R. Descartes, Discourse on Method, Part 5)

1. Introduction

When an infant learns to handle a new object, through the observation of another or through direct experience, her motor repertoire is enriched with a new *sensorimotor* representation of an action. What is the role of this kind of representation in the way an individual represents that action conceptually?

The influence of sensorimotor experience on cognition is acknowledged in all theories of concepts. Although the so-called *classic* theories hold that concepts are stored in the form of abstract representations or symbols within dedicated cerebral structures, remote from the modality-specific mechanisms for perception and action (Fodor, 1975, 1983; Kintsch, 1998; Landauer & Dumais, 1997; Pylyshyn, 1984; Shallice, 1988), these theories acknowledge that symbolic representations can be shaped by sensory and motor experience. For instance, in the Sensory/Functional Theory (Warrington & McCarthy, 1983, 1987; Warrington & Shallice, 1984), the organization of object concepts is constrained by the modality through which individuals typically interact with the physical objects (i.e., sensory/perceptual or motor/functional), resulting in subsystems that parallel the sensory and motor modalities of input and output. On another account, conceptual organization is held to align with object domains (possibly: animals, conspecifics, plant life, and tools) that reflect aspects of the environment that were relevant in our evolutionary history (Caramazza & Shelton, 1998; Carey, 2009; Carey & Spelke, 1994). A third class of theories builds on the Correlated Structure Principle, whereby different categories of objects are defined in the semantic memory as a set of features or properties that co-occur regularly in the world (Caramazza, Hillis, Rapp, & Romani, 1990; Devlin, Gonnerman, Andersen, & Seidenberg, 1998; McClelland & Rogers, 2003; Tyler & Moss, 2001). Although these accounts differ in many respects (for extensive reviews of the theories of concepts, refer to Mahon & Caramazza, 2009; Martin, 2007), they share the distinctive stance that concepts, while tied in important ways to sensory and motor systems, are more abstract than the token-based information contained within sensory and the motor systems.

Sensorimotor experience is assigned a more substantial role in embodied approaches to cognition. Although lacking a unique definition (see Chrisley & Ziemke, 2002; Wilson, 2002), the idea of "embodiment", dating back to the mid-1980s, has been developed in cognitive science and artificial intelligence, promoting the view that physical experience with the world is a *condition sine qua non* for any form of intelligence or knowledge (Pfeifer & Scheier, 1999), and that the sensory and motor features of entities (e.g., objects or actions) are the core attributes of their conceptual representation. This view stems from Motor Theories of Cognition (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Watson, 1913; see for an overview, Scheerer, 1984), according to which conceptual meaning results from bodily interaction with the environment and from the human capacity to project from sensorimotor and social experience to conceptual structures (Lakoff & Johnson, 1980, 1999). One classic example is the concept of "grasping the idea", which would be grounded in the bodily experience of grasping a physical object with one's own hand.

The latest embodied theorization was articulated by Allport (1985), who proposed that neural processes encoding the physical attributes of an object presented to senses constitute the basis of the conceptual representation of that object. On this view, conceptual knowledge is represented by neural systems dedicated to perception and action, such that comprehension requires the *re-enactment*, or the internal *simulation*, of the sensory and motor (and emotional) processes that are engaged in typical interaction with the entity to which the concept refers (see Barsalou, 1999; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Prinz, 1997; Zwaan, 2004).

The *simulationist* approach to semantics has gained support from the discovery of mirror neurons in the macaque brain, a neural population that might subserve a so-called *mirror matching* mechanism, providing a potential explanation for how action meets cognition. Mirror neurons, originally found in the macaque premotor area F5, respond to a given action, regardless of whether it is executed by the macaque itself or observed while performed by a third agent, i.e., a co-specific or the experimenter (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The observation-execution matching mechanism supported by mirror neurons might provide a physiological foundation to the simulation theory, as it suggests that action understanding results from the direct mapping of a perceived action onto the perceiver's motor system (Rizzolatti, Fogassi, & Gallese, 2001). Perhaps more strikingly, in the same area F5, neurons were found with action-audition *mirror* properties: the same neurons fired when the monkey performed an action (i.e., breaking a peanut) and when the sound associated with that action was heard (Kohler et al., 2002). These findings first suggested that the mirror matching could encode the action-related information in a modality-neutral or modality-independent manner.

In humans, the existence of neurons with mirror properties remains controversial, possibly due to the limitations of the available neuroimaging techniques (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Dinstein, Thomas, Behrmann, & Heeger, 2008; Lingnau, Gesierich, & Caramazza, 2009; Turella, Pierno, Tubaldi, & Castiello, 2009); however, it has been argued that the human motor system contains a mirror matching mechanism that supports understanding actions that are perceived through the senses or implied by language. In particular, a large body of studies have shown that action-related stimuli, including words, may activate sensorimotor regions, motivating the claim that perceived actions are mapped into the sensorimotor representation of the implied physical act, and understood via motor simulation (see for reviews, Feldman & Narayanan, 2004; Pulvermüller & Fadiga, 2010; Rizzolatti & Craighero, 2004).

In the first place, it is useful to consider what an action is: the agent's intentions and her goals? A motor act with specific parameters (path, manner, force, posture and so on)? Its effect on the environment and/or on other entities (individuals or objects)? An action is all these things such that understanding an action is to integrate all or some of these aspects into a coherent representation. No theory of concepts denies this; what truly distinguishes the embodied approach from the "disembodied" one is the extent to which the ability to categorize/recognize an action can be captured by the encoding of its sensorimotor dimensions. It is beyond the scope of this review to establish which existing theory, as a whole, best account for how action concepts are organized and represented in the brain; however, the results from different lines of research can provide important insights into the relevance of sensorimotor information in the mental representation of actions. In this review, we will focus on the processing of action-related words as one medium to access the conceptual system: our objective is to assess the weight of sensorimotor input in the way words expressing sensorimotor relations are acquired and represented. This analysis highlights two forms of empirical evidence that can be brought to bear in evaluating the claim that sensorimotor information substantially contributes to the conceptual representation of actions.

2. Sensorimotor representations and language understanding

A tradition of psycholinguistic research has documented the influence of language processing on motor behavior, and vice versa (see for reviews, Anderson, Chiu, Huette, & Spivey, 2011; Barsalou, 2009). A frequent observation, held to reflect the *embodiment* of language, is the facilitation of motor responses (e.g., moving the arm away from the body) following the presentation of utterances describing congruent motor acts (e.g., "Vittorio delivered the pizza to you"; Glenberg & Kaschak, 2002). Although compatibility (or congruence) effects can be elicited by different word classes (e.g., nouns; Tucker & Ellis, 2004; adjectives; Gentilucci & Gangitano, 1998), in a sentential context, the verb is the linguistic element that typically triggers motor facilitation (Zwaan & Taylor, 2006). Accordingly, verbs are considered the prototypical class of action words, whereby information about an action is conveyed not only through the semantics of a verb, but also through its argument structure eliciting relations between elements, such as an agent who is acting over something/someone else (Gillette, Gleitman, Gleitman, & Lederer, 1999).

Neuroimaging studies have found activations in the left primary motor (M1) and premotor regions, when participants processed action verbs (Hauk, Johnsrude, & Pulvermüller, 2004) or sentences (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Boulenger, Hauk, & Pulvermüller, 2009; Tettamanti et al., 2005). Transcranial magnetic stimulation (TMS) to the left M1 during action-language processing increased motor activity (or facilitation), as measured by motor-evoked potentials (MEPs), in peripheral muscles responding to the stimulated area (Glenberg et al., 2008; Oliveri et al., 2004). These and similar findings (see for reviews, Borghi, Giannelli, & Scorolli, 2010; Fischer & Zwaan, 2008; Pulvermüller & Fadiga, 2010) are taken as evidence that motor information is automatically retrieved during action-word understanding (Pulvermüller, 2005).

On the other hand, a number of studies suggest that the mapping of an action-word meaning onto a corresponding motor program is not automatic, but relies on factors such as the task demand (Papeo, Vallesi, Isaja, & Rumiati, 2009; Tomasino, Werner, Weiss, & Fink, 2007; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008; Willems, Hagoort, & Casasanto, 2010), or the overall sentential context in which an action word is encountered (Papeo, Corradi-Dell'Acqua, & Rumiati, 2011; Raposo, Moss, Stamatakis, & Tyler, 2009; Rüschemeyer, Brass, & Friederici, 2007). For instance, it has been observed that task contexts driving participants' attention toward the motor meaning of the word (e.g., judging the semantic relation of a word with a bodily action) activate early motor structures (i.e., left M1) more consistently than tasks in which the access to meaning is less explicit or only incidental (e.g., counting the number of syllables in a verb; Papeo et al., 2009). Modulation of neural activity according to task demands (lexical decision vs. explicit imagery on verbs) has been reported also in higher-order motor regions, such as the premotor cortex (Willems, Toni, Hagoort, & Casasanto, 2010). Thus, while there is little doubt that the conceptual processing of actions can encompass sensorimotor regions; researchers have raised the question as to whether this activity is automatic for understanding. The focus on the automaticity of motor activation is motivated by a wealth of behavioral evidence suggesting that conceptual representations are retrieved automatically when we hear or read words, irrespective of the task (Neely, 1991; Stroop, 1935). Therefore, automatic activation of motor regions during word exposure would be a relevant cue that sensorimotor information substantially contributes to the semantics of action words.

The literature in the field appears mostly led by neurimaging and behavioral studies on healthy adults, granting that sensorimotor regions or processes can be recruited during action-word understanding, without however clarifying what their relevance is. In the current review, we will evaluate the *weight* of sensorimotor information in word understanding, by taking advantage of cognitive neuropsychology and infant studies that, more or less directly, have addressed this issue. If the human mind is regarded as a tower, studying the way it is erected (infant studies) and the way it one day may collapse (patient studies) can help us identify what constitutes its foundations. On the one hand, "the child provides the only opportunity that we have to observe language in its nascent state" (Jakobson, 1941/1968); in this context, infants' studies provide a window into the relevance of sensorimotor information related to objects and events, in verb acquisition. On the other hand, the study of neuropsychological populations provides a perspective on the cognitive consequences of damage to either the language or the motor system. In particular, with the neuropsychological approach, we can assess whether and how a breakdown in the system for action performance impacts action-word processing and, vice versa, how damage to the semantic representation of action words affects patients' ability to perform purposeful actions. A cross-talk between the two fields that deal with the very same structure (i.e., the human mind), can strengthen the conclusions drawn by each field on its own, promoting a critical consideration of the relationship between modality-specific (motor) and central (conceptual) processes. In reviewing neuropsychological and infant studies, we will point out a number of facts revealing how sensorimotor information carries a relatively little weight in the way words are acquired and represented in the brain.

3. What damaged brains tell about the role of sensorimotor representation in action-word understanding

In neuropsychology, the idea that language is closely interwoven with the motor function dates back at least to the 19th century, when scientists suggested that the damage to a single central system for communication could be responsible for both aphasia, i.e., a disturbance of the language function, and apraxia, i.e., the disorder in executing purposeful actions (Finkelnburg, 1870; Goldstein, 1948; Head, 1926; but see Geschwind, 1965; Wernicke, 1874). Today, it remains debated whether aphasia is a domain-specific deficit or is part of a more general impairment affecting other domains beyond language (Goldenberg, Hartmann, & Schlott, 2003).

That line of research now offers relevant insight into the questions raised by more recent interest in embodied approaches to cognition. Notice that, although in most studies on the relationship between aphasia and apraxia, word-stimuli (particularly, verbs) were not explicitly categorized along the semantic dimension of "manipulability" (i.e., how much their meaning relates to a bodily action), their processing was tested with picture naming or word-picture matching. These tasks involve visual presentation of events, and therefore favor the selection of verbs with concrete (*to eat*), rather than abstract (*to adore*) meaning. Therefore, it seems reasonable to start considering the relationship between the patients' ability to perform actions and their ability to process words, by taking advantage of that literature.

In this section, we will first review evidence linking verb processing to the left inferior frontal gyrus (LIFG), a region that has also been related to action observation, imitation and action knowledge. We argue that although action and verb processes may overlap anatomically in the LIFG, this does not answer at all the question of what the role of sensorimotor representation is in verb processing. We will then discuss a number of facts, such as neuropsychological double dissociations, that challenge the notion that sensorimotor information is the core attribute of action-word representations, and that require researchers to *re*-think the relationship between action and language systems.

3.1. Verbs and actions in the left inferior frontal gyrus

The monkey area F5, where mirror neurons were first found, is the homologue of the language-related Broca's region, located in the LIFG of the human brain: F5 and Broca's region have analogous location within the frontal cortex (i.e., in the inferior precentral cortex), and exhibit cytoarchitectonic similarities (Petrides & Pandya, 1994). Evidence that both verb processing and action processing involve the LIFG has suggested that verbs enjoy a special relation with actions. On the one hand, selective deficits in verb production (vs. noun) have been consistently associated with agrammatic form of aphasia (or Broca's aphasia) and damage to left frontal structures, such as the LIFG (e.g., Caramazza & Hillis, 1991; Damasio & Tranel, 1993; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; McCarthy & Warrington, 1985; Miceli, Silveri, Nocentini, & Caramazza, 1988); deficits in verb comprehension have been also associated with damage to the LIFG (Cotelli et al., 2006; Hillis et al., 2006). On the other hand, neuroimaging studies have linked the same region to the processing of action during observation (Decety et al., 1997; Rizzolatti et al., 1996) and imitation (Iacoboni et al., 1999; Koski et al., 2002). In line with these results, a recent study involving 147 left- and right-damaged patients found that, in the three cases with left-sided damage and impairment across a range of tasks used to assess lexical and conceptual knowledge of actions (i.e., naming, word-picture matching, attribute judgments on words and pictures, and associative comparisons on words and pictures), the lesion was centered in the LIFG (Kemmerer, Rudrauf, Manzel, & Tranel, in press). In the same vein, a lesion study suggested that the involvement of this region in word processing depended on the degree to which a word's meaning was associated with a goal-directed movement (Arévalo et al., 2007).

However, a number of considerations challenge the conclusion that, by virtue of their anatomical overlap, action and verb processing are functionally dependent. First, verb deficit does not necessarily result from damage to LIFG. Mätzig, Druks, Masterson, and Vigliocco (2009) found that 9 of 36 patients tested in their study exhibited verb deficits with spared frontal regions, and only in two cases was the verb deficit associated with damage to LIFG. Most importantly, the relationship between this brain region and verb processing does not imply a role of sensorimotor processes in language understanding, as LIFG can be barely defined as a "sensorimotor" region. If any action-related information is held in there, it is likely to be at a level more abstract than the specification of the sensorimotor features for action production. One clear observation in favor of this argument is that the neural activity in LIFG does not distinguish between action-meanings related to different body parts (i.e., mouth, hand, foot; Tettamanti et al., 2005; see also Kemmerer & Gonzalez Castillo, 2010).

Second, it is far from clear whether the recruitment of LIFG in verb processing reflects the retrieval of semantically relevant action-related information, or rather relates to morpho-syntactic computations and/or executive control. In fact, fMRI studies revealed greater LIFG activity for verbs than for nouns when participants performed semantic judgments on inflected forms of the words, but not when the task involved the same words presented in their uninflected form (Longe, Randall, Stamatakis, & Tyler, 2007; see also Siri et al., 2008; Tyler, Bright, Fletcher, & Stamatakis, 2004). Moreover, following evidence for the involvement of LIFG in a surprisingly large range of tasks, some scholars have argued that this region could maintain an executive-*like* function (Hagoort, 2005). This hypothesis would also be compatible with the more consistent association of LIFG with verb, relative to noun processing: since verbs are morphologically and morpho-syntactically more complex than nouns, they could pose a greater demand to executive resources and, in the event of brain damage, be more vulnerable to limitation of executive resources (Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Tyler et al., 2004; Vigliocco et al., 2006).

3.2. Associations of language and sensorimotor processes

Studying language abilities in neurological patients with impaired motor performance appears to be the most obvious testbed for the hypothesis that the sensorimotor information related to an action is one core attribute of the semantics of action-related words.

Due to the high incidence of cerebrovascular accidents worldwide (Hachinski, 2002), stroke patients are the pathological population the most commonly studied by cognitive neuropsychologists. In these patients, impairment in executing purposeful actions (i.e., apraxia) often results from damage to the left hemisphere and co-occurs with aphasia. Neuropsychological studies have routinely reported correlations between the severity of aphasia and the severity of apraxia, and between deficits in language abilities, action knowledge and action performance (De Renzi, Pieczuro, & Vignolo, 1968; Dee, Benton, & Van Allen, 1970; Hecaen, 1962; Kertesz & Hooper, 1982; Liepmann, 1905). For instance, in groups of aphasics, language performance was found to correlate with the ability to execute pantomimes of tool use (Goldenberg et al., 2003), and to execute naturalistic actions involving technical devices (e.g., making coffee; Hartmann, Goldenberg, Daumüller, & Hermsdörfer, 2005). Duffy and colleagues (Duffy & Duffy, 1981; Duffy, Duffy, & Pearson, 1975) reported that linguistic deficits in a group of 47 aphasics were tightly correlated with deficits in pantomime expression as well as in pantomime recognition. Even when motor performance is spared, impaired gesture recognition is a common correlate of language deficit (see also Daniloff, Noll, Fristoe, & Lloyd, 1982; Ferro, Santos, Castro-caldas, & Mariano, 1980; Varney, 1978). Gainotti and colleagues (Gainotti & Lemmo, 1976; Gainotti, Caltagirone, Masullo, & Miceli, 1980) observed that nonverbal abilities such as gesture recognition were the poorest in patients with pronounced lexical-semantic impairments, suggesting a direct link between lexical-semantic processing and action representation.

Along with the association between aphasia and impairments in gesture production and recognition, there is evidence that damage to the motor system can be accompanied by language impairment. In the abovementioned study by Kemmerer et al. (in press), lesions encompassing the primary motor and the premotor cortices were reported in patients with specific deficits in action naming and action-word comprehension. The involvement of the motor system in language has been further inferred from the study of individuals with neuropathology affecting the cortical and subcortical structures involved in action organization and motor control. Cotelli et al. (2006) found that 10 patients with corticobasal degeneration (CBD), a subtype of fronto-temporal dementia characterized by the atrophy of bilateral premotor cortices, superior parietal lobes, and striatum, exhibited a prominent limb apraxia and were severely affected in naming manipulation (vs. non-manipulation) actions. Bak et al. (2006) reported selective impairment of verb processing in two individuals with a motor disorder resembling progressive supranuclear palsy, and problems in the production and comprehension of verbs (vs. nouns) in 5 out of 6 patients with Motor Neurone Disease (MND), a neurological condition affecting motor neurons (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001).

While demonstrating co-occurrence of motor disease and language impairment, none of these studies could ascertain that the former was responsible for the loss of verb knowledge, or language abilities more generally. In the study by Kemmerer et al. (in press), no patient was reported with deficits in action-word production and comprehension and *selective* damage to motor/premotor regions; importantly, in all cases of verbal impairment, the LIFG was also affected by the lesion. In the study by Bak et al. (2001) on MND patients, the semantic dimension of the stimuli was confounded with the grammatical class, as verbs and nouns were not matched for their meaning (i.e., action-related vs. nonaction-related); thus, it is not possible to establish whether the verb impairment reflected a semantic, a grammatical or a morphosyntactic deficit. Moreover, in MND patients, including those of Bak et al., the atrophy of frontal lobes extending much beyond the motor regions casts serious doubt on the motor origin of language disorder (see Hickok, 2010; Neary et al., 1990).

To establish a causal relationship between language understanding and the neural mechanisms for action performance, one needs to preclude the possibility that the association of symptoms reflects damage to contiguous structures subserving different functions. The association of symptoms may also result from damage to a third function, critically involved in both processes. These alternative explanations earn credence given that associations of impairments in language and motor functions are not universally found in groups of patients (Bell, 1994; Goodglass & Kaplan, 1963; Wang & Goodglass, 1992).

3.3. *Dissociations between language understanding and sensorimotor processes*

Evidence of correlated performances based on group analyses, while reflecting the general trend of a group, may run the risk of masking dissociations in individual cases that go against this group-level tendency (Caramazza, 1986; Shallice, 1988). Avoiding this *average artifact* requires analyzing the performance of single patients: a double dissociation, whereby Case 1 is impaired (or more impaired) on task A vs. task B and Case 2 shows the opposite pattern of performance, provides the most solid basis for making inferences about the organization of cognitive abilities in the brain, and processes in computational models (Shallice, 1988). Should a double dissociation be observed, with Case 1 showing apraxia but preserved action-language comprehension, and Case 2 having impaired action-language comprehension but spared praxis, this would be evidence that the two functions rely on independent systems. Therefore, to take advantage of the cognitive neuropsychology methodology to support the functional dependence between language and motor systems, one should be able to show not only that the deficits in action-word comprehension and action performance are associated in groups' of patients, but also that a double dissociation between the two tasks does not occur across the range of cases studies.

Dating back to the early 20th century, the analysis of single patients' performance revealed cases of left-damaged patients with apraxia or right-sided motor dysfunction (e.g., hemiplegia) in the absence of aphasia (Liepmann, 1905), and cases of severe aphasia with normal praxis abilities (Kertesz, Ferro, & Shewan, 1984). The early study by De Renzi, Motti, & Nichelli (1980) already exemplified the limit of group-level correlations. The authors observed that, although the imitation scores of 100 left-damaged patients correlated positively with their verbal competence (measured with the Token test), this correlation was not particularly high, and was likely to depend on the contiguity of the underlying nervous structures. Moreover, at the single-case level of analysis, 12 of the 60 aphasics in the sample were not impaired in imitation, and two of the 40 non-aphasics were selectively impaired in imitation. Likewise, in a sample of 699 left-damaged patients, Papagno, Della Sala, and Basso (1993) observed 10 non-aphasics who failed to imitate symbolic and nonsymbolic actions, and 149 non-apraxics with aphasic deficits, as assessed with standard examinations of production, comprehension, repetition, writing and reading of both words and sentences. More recently, in a group of 61 left-damaged patients, Mengotti et al. (2009) reported 6 cases of selective language impairment and 5 cases of pure ideomotor apraxia. The functional independence of language and praxis functions was supported by their anatomical segregation: using the Voxel-based Lesion Symptom Mapping (VLSM) on the same sample, the authors found that the imitative deficit was associated with lesion to the angular gyrus and the bordering white matter, while aphasia was associated with damage to the superior temporal cortex.

As observed earlier, these studies were framed within the debate on whether aphasia is a domain-specific or a domain-general disorder (see e.g., Finkelnburg, 1870) and, therefore, considered the relationship between apraxia and any aphasic symptom, instead of specific impairments of action-language comprehension. However, although they cannot be taken as direct assessment of the prediction that representations supporting action execution are central to the semantic representation of action language, they provided initial insight on the relationship between the language and motor disorders in neurological populations. The overall picture from that line of research suggests that nonverbal impairments are highly variable among aphasic subjects: in the range of possibilities, there are aphasics who exhibit effective motor behavior and nonverbal competence.

More directly relating to the debate on the embodiment of language, Saygin, Wilson, Dronkers, and Bates (2004) proposed that verbal and nonverbal representations of action share substrates to a variable degree, depending on how much verbal and nonverbal tasks have in common in terms of perceptual and conceptual properties and the developmental stage in which the involved abilities are acquired (Saygin et al., 2004; see also Bates & Dick, 2002). Following this proposal, they tested the ability of 29 aphasics in verbal and nonverbal action comprehension using identical action-stimuli. Transitive pantomimes were depicted in line drawings or described by sentences; participants (patients and controls) had to choose between two alternatives the object involved in the action, which was not shown in the line drawings, and nor labeled in the sentences. The authors found that the performances on the two tasks did not correlate when considering the whole group of 29 aphasics, but they did in a subgroup of them. While emphasizing evidence for symptom association, the authors attributed the overall lack of correlation to reading being acquired much later in life than nonverbal action competence.

Although in the study of Saygin et al. (2004), action-language comprehension was not compared with action production, the authors' logic would predict that word and sensorimotor representations overlap maximally when the two relate to the same action and are assessed with tasks that involve abilities acquired at equally early stages of cognitive development. The potential of this hypothesis to solve or, at least, to orient the dispute between associative and dissociative views in neuropsychology, led Papeo, Negri, Zadini, and Rumiati (2010) to directly test it in a multiple single-case study on 12 consecutive left-damaged patients. Patients' sensorimotor skills were tested with action imitation and tool use, while the lexical-semantic processing of action-words, including action-verbs and tool-nouns, was tested with picture naming and name-to-picture matching. Like action-verbs, tool-nouns are considered action-related words: sensorimotor regions have been also implicated in the processing of this word class, possibly because of the close association of a tool representation with a specific motor program (Chao & Martin, 1999; Grabowski, Damasio, & Damasio, 1998). In Papeo et al. (2010), motor and linguistic tasks, involving the very same action- and tool-stimuli, were chosen taking into account evidence from developmental studies, that the motor ability to perform deictic gestures, gestural routines and tool use develops synchronously with the acquisition, and particularly the comprehension, of single-words (Bates & Dick, 2002; Lenneberg, 1967; Siegel, 1981). In other word, when selecting language and praxis tasks, Papeo et al. considered the age of acquisition of the underlying abilities as a relevant factor that could maximize the functional overlap between word comprehension and motor production.

Despite matched factors at stimulus- and task-levels, single-patients' performances revealed double dissociations between the ability to retrieve and comprehend action-verbs and tool-nouns and both the ability to imitate actions and to use tools. That is, the lexical-semantic representation of action words was independent from the basic ability to translate visual input into motor output for imitation, and from the ability to produce learned object-associated actions (Papeo et al., 2010). In the same vein, a recent lesion study on 27 left-stroke patients found no causal effect of damage to mouth/hand/foot sensorimotor and somatosensory cortices on the ability to recognize verbs and nouns related to mouth/hand/foot actions (Arévalo, Baldo, & Dronkers, 2010). Moreover, the authors observed that when damage to those regions occurred, it did not block patients' ability to process action words, suggesting that the network responsible for action execution is neither sufficient nor necessary for the comprehension of action words.

Previous neuropsychological studies have reported dissociations between action performance and the visual recognition of actions and objects, or their conceptual knowledge (Cubelli, Marchetti, Boscolo, & Della Salla, 2000; Mozaz, Rothi, Anderson, Crucian, & Heilman, 2002; Ochipa, Rothi, & Heilman, 1989; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Rosci, Valentina, Laiacona, & Capitani, 2003; Rothi, Ochipa, & Heilman, 1991, Rumiati, Zanini, Vorano, & Shallice, 2001; see Mahon & Caramazza, 2005, for a review). For instance, in a group on 37 stroke patients, Negri et al. (2007) tested the ability to recognize visually presented tools, to use them and to imitate the associated tool-use pantomime. The authors reported cases with apraxia and preserved action and object recognition, and others with no apraxia and impaired visual action and object recognition (i.e., visual agnosia; see Mahon et al., 2007, for the lesion analysis on this group of patients). In the light of all these studies, praxis abilities are not required for action recognition, as was the case for action-language understanding.

If language-related motor activation reported in neuroimaging literature is taken as evidence for a simulationist account of language, then the prediction for neuropsychological observations should be that: (1) a patient with deficit in action-word understanding is impaired in performing the implied language actions (and vice versa); and (2) these cognitive deficits can result from damage selectively affecting motor/premotor regions. To the best of our knowledge, no one single patient has so far been reported who fits both conditions. The current literature instead suggests that the semantic definition of an action word, such as a verb, does not correspond to the representation of the most concrete (sensorimotor) aspects of the implied motor act. In our metaphor, the tower does not collapse when sensorimotor representations are damaged, suggesting they do not belong to its foundations. In the next section, we will assess the strength of this conclusion considering how the tower is erected: we will show how the processing of sensory and motor features of actions and events are insufficient to account for the complexity of verb learning in infants, and how this process, instead, relies on a complex interplay between sensorimotor experience, conceptual dimensions and syntactic features.

4. What learning minds tell about the role of sensorimotor representation in action-word understanding

Early verb learning requires infants to map a novel word onto an action they are carrying out or perceiving. Actions are multidimensional events involving a set of sensorimotor and kinematic features (e.g., force, direction, effector, posture, repetition), as well as goals and intentions that go beyond the mere perceptual and motor aspects of an action. We will review a number of studies showing how young infants privilege the latter over the former dimensions when learning a verb meaning.

While, in the first year of life, word learning may be described as forming an association between a sensory or motor input and a linguistic label, the engagement of more complex and efficient mechanisms becomes evident in older infants (Hochmann, submitted for publication; Lock, 1980; McShane, 1979; Stager & Werker, 1997). By the end of the second year of life, infants reach a productive vocabulary of about 50 words and enter a *vocabulary spurt*, where they begin to learn words at very fast rate (Carey & Bartlett, 1978; Golinkoff, Church Jacquet, Hirsh-Pasek, & Nandakumar, 1996; Golinkoff, Hirsh-Pasek, Bailey, & Wenger, 1992; Heibeck & Markman, 1987). At this stage, it is now known that the acquisition of novel words involves a series of conceptual constraints that theories based on mere perceptual/sensorimotor input-label association cannot account for (Halberda, 2003; Hochmann, Endress, & Mehler, 2010; Markman, 1990; Markman & Hutchinson, 1984; Markman, Wasow, & Hansen, 2003; Mervis, 1987; Soja, Carey, & Spelke, 1985).

Verb learning starts in this same period and, relative to noun learning, appears to be a harder task. Indeed, this process can be evidenced in experimental environments only with infants older than 23-months (Bernal, Lidz, Millote, & Christophe, 2007; Golinkoff & Hirsh-Pasek, 2008; Naigles & Kako, 1993), almost ten months later than reliable experimental noun teaching (Werker, Cohen, Lloyd, & Casasola, 1998). One reason for this difficulty may be that verbs need to map onto complex events, rather than simple objects. In fact, even considering the *simplest* case of a verb denoting a concrete, visible action, its interpretation involves a complex set of event knowledge including perceptual components, such as the description of typical participants and their motion, means, time course and duration, but also more abstract components such as causal relations and intentionality (Zacks & Tversky, 2001). To understand which components are the most relevant for the representation of a novel action verb to settle in the infant's brain, we can earn first insight from understanding how infants perceive events that verbs refer to.

4.1. Infants encode observed actions in terms of goals and intentions

Before understanding the meaning of any verb, infants perceive and represent structured events. Verb learning is likely to build on these representations. Thus, one way to approach the question of how infants learn verbs, or what are the "rudiments" of a verb meaning, is to investigate whether infants' encoding of perceived actions principally consists of sensory and motor processes or more conceptual dimensions. The available results show that infants are sensitive to the perceptual features of action, such as path and manner (Lakusta & Landau, 2005; Pruden & Hirsh-Pasek, 2006; Pulverman & Golinkoff, 2004), but are also capable of encoding abstract dimensions, such as the goals and the causal relations between subevents (Ball, 1973; Carey, 2009; Kosugi, Ishida, & Fujita, 2003; Muentener & Carey, 2006; Spelke, Phillips, & Woodward, 1995), and to distinguish between roles of agent and patient participating in a motor scene (Leslie, 1982; Pauen and Träuble, 2009; Saxe, Tenenbaum, & Carey, 2005; Saxe, Tzelnic, & Carey, 2007).

First, studies on imitation have provided evidence that infants represent the goals of actions. Gergely, Bekkering, and Király (2002) proposed that 14-month-olds imitate the means of a goal-directed action, only when they consider it to be the most rational alternative to achieve the goal. Observing an experimenter pushing a button with the head, infants imitated the head action if the experimenter's hands were free, but not if they were occupied holding a blanket. These results suggested that infants performed a rational analysis of the event, inferring from the hand-free condition that the head was the right effector with which to push the button (otherwise the experimenter would have used her free hands), and from the occupied-hands condition that the head was only a surrogate of the more classical hand effector, not used by the experimenter only because occupied. According to this interpretation, action understanding is not based solely on the encoding of a motor program that infants can perform, but involves reasoning about rationality, goals and intentionality of the agent. More recent studies, however, pointed out that 14-month-olds may not be able to execute the head-touch action without supporting their weight with their hands pressed on the table (Paulus, Hunnius, Vissers, & Bekkering, 2011a, 2011b). This observation leaves open a possibility that, in Gergely et al. (2002), the infants' failure to imitate in the occupied-hand condition was due to their inability to perform the action, leading to an inability to accurately represent it (but see Gergely, Chen, & Király, 2011).

Other studies use infants' looking times as dependent variable, thus switching from action imitation to action perception. This methodology has the advantage of removing the potential performance limitations caused by infants' restricted motor repertoire. Measuring the looking times, it was shown that infants, habituated to a scene where the agent's movements were constrained by physical obstacles in the environment (i.e., the agent moved around an obstacle that impeded a straight path), were surprised (i.e., longer looking times) when the environmental constraints were removed but the agent did not choose the straight path to the final location (Gergely & Csibra, 2003; Gergely, Nádasdy, Csibra, & Bíró, 1995; Kamewari, Kato, Kanda, Ishiguro, & Hiraki, 2005; see also Csibra, 2008; Southgate, Johnson, & Csibra, 2008). These findings suggested that infants encode the goal of an agent's motion (i.e., reaching a given location), rather than its physical properties (i.e., the path). The goal is an abstract property, which does not correspond to, but is inferred from the perceptual and motor features of that action.

Already at five-months, infants are capable to attribute goals to actions. In a seminal work, Woodward (1998) habituated five-month-old infants to a scene where two objects (a teddy bear and a ball) were presented, and the hand of the experimenter repeatedly reached for only one of them (the teddy bear). When the two objects switched positions, infants looked longer (indicating the detection of a novel or unexpected event) if the hand kept on following the same path and reached the second object (the ball) compared to when the path was altered to reach the original goal (the teddy bear). These results suggest that, in the habituation phase, infants encoded the action in terms of goal (reaching the teddy bear), rather than in terms of sensorimotor features (the path). Interestingly, the intentionality underlying action performance appears critical for infants to encode the goal: in a follow-up experiment, when the experimenter's movements were unintentional (i.e., she flopped her hand onto one of the toys unintentionally), infants did not look longer for the novel-goal event (Woodward, 1999). Thus, when intentionality and goals are involved, infants privilege these abstract dimensions in order to encode and then recognize the action.

How do infants realize that an action is intentional and goal-directed? Recent research suggests that infants' first-person experience plays a role in this process. Woodward and colleagues observed that infants encoded a goal (i.e., they looked longer to a movement toward an unexpected goal), only when they could produce the perceived action themselves (Woodward, 2009). For example, only 9-month-old infants who were able to perform pointing, but not those who were not could understand another's pointing action as object directed (Brune & Woodward, 2007; Woodward & Guajardo, 2002). Likewise, the ability to pull a cloth in order to reach an object that is supported by it and the ability to understand the goal of the same action performed by another develop in parallel between 10- and 12-months of age (Sommerville & Woodward, 2005).

Is the correlation between action performance and action understanding sufficient to argue for a causal relation between the two? Sommerville, Woodward, and Needham (2005) addressed this question in a study involving two groups of 3-month-olds, who are not yet able to manually reach for objects. One of the two groups was equipped with velcro-covered "sticky mittens", while experiencing reaching for objects; infants in this group – but not in the other – interpreted as object-directed the unusual reaching action performed by another equipped with sticky mittens, thus, suggesting that action performance contributed to action understanding.

These results show that sensorimotor experience does play a role in infants' learning about goal-directed actions; precisely, infants seem to attribute goals to actions that they can perform. It is unclear, however, how infants as young as 3-months could have learned the *abstract* notion of goal itself, especially when considering that at that age they cannot grasp objects intentionally. In the "sticky mittens" experiment, infants must first generate the goal to reach for objects; then, by acquiring specific movements, they learn how to fulfill that goal. The learnt association between an inner goal and an action to achieve it, can thus help infants to attribute a goal to another, when they recognize the action that the other is performing. We emphasize here how this learning process implies that a goal pre-exists relative to the motor program to achieve it; in other words, that motor experience, by 3 months of life, cannot account for the acquisition of the notion of goal. Accordingly, it has been observed that some non-performable actions can be assigned a goal: at 6-to-8 months, infants can accept also biologically impossible movements as well-formed goal-directed actions (Southgate et al., 2008). It seems likely, in the light of these results, that infants have a priori representations of goals and desires, which they combine with representations derived from sensorimotor experience, to learn about others' actions and goals (Meltzoff, 2007).

4.2. *Conceptual and syntactic constraints on verb learning*

When infants learn a novel verb referring to an action, do they map a motor program (path and manner of motion) onto a linguistic label, or do they privilege higher-level abstract properties of that action (e.g., goals, causality)? In other words, does the bias toward goals and intentions observed in infants' action perception, apply to verb learning? One intriguing observation is that the motor dimensions of actions are differently encoded in different languages. For example, Spanish and Greek learners interpret a novel verb referring to a movement in terms of path of motion, while English learners favor the manner of motion (Hohenstein, Eisenberg, &, Naigles, 2006; Naigles & Terrazas, 1998; Papafragou & Selimis, 2010). This could be taken to suggest that both path and manner are optional dimensions and not the core attributes of verb meanings.

More specifically, there is evidence that several *conceptual* biases constrain noun and verb learning. In acquiring both word classes, infants apply the mutual exclusivity assumption, whereby they map a novel verb onto a novel action rather than onto another that has been already associated with a different label (Merriman, Evey-Burkey, Marazita, & Jarvis, 1996). Moreover, Golinkoff, Hirsh-Pasek, Mervis, Frawley, and Parillo, (1995) proposed that verb learning relies on the "categorical scope" principle, according to which an action word can be readily extended to an action of the same type, regardless of the agent and the superficial differences in the manner the action is performed (see Forbes & Farrar, 1993; Golinkoff et al., 1996). The existence of this principle in word learning supports the idea that the referent of a verb is not principally encoded as a motor program, but in terms of properties that are abstract enough to be generalized to novel instances of the same action. Forbes and Poulin-Dubois (1997), for example, showed that 26-month-olds could extend the verb *pick up*, typically associated with a hand action, to a goal-directed action realized by a novel agent with its foot, but not to an action with a different goal, although realized with the hand. This basic mechanism allows us to label as "jump" the action executed by Mike Powell when beating the long-jump world record, as well as that of a kangaroo, despite the two acts relying on *quite* different motor programs.

Besides conceptual biases, a verb's meaning can be constrained by the syntactic construction (e.g., transitive, intransitive, ergative) in which a verb is encountered. In a seminal study by Gillette et al. (1999), adults were presented with short silent movies of child–mother interactions and were instructed to guess what word was uttered when a 'bip' sound was heard. Results showed that participants were unable to guess the meaning of a novel verb unless they were also provided with the syntactic structure in the form of a sentence with nonsense nouns and verbs. This and similar phenomena gave rise to the "syntactic bootstrapping" theories of language acquisition, holding that infants use syntactic information to constrain the interpretation of a novel word (Bunger & Lidz, 2004, submitted for publication; Fisher, 1996, 2002; Fisher, Gertner, Scott, & Yuan, 2010; Gillette et al., 1999; Gleitman, 1990, 1994; Gleitman & Gleitman, 1992; Landau & Gleitman, 1985; Naigles & Kako, 1993; Naigles, 1990; Papafragou, Cassidy, & Gleitman, 2007).

Accordingly, Naigles and Kako (1993) showed that infants as young as 23-month-olds are already aware that transitive verbs typically map onto causative actions, and intransitive verbs onto intransitive actions. The authors presented infants with a scene where a duck was pushing a bunny, while both actors were carrying out the same arm movement. The novel verb "*gorping*" describing the scene was taught to two groups of infants: infants who heard "the duck is *gorping* the bunny" mapped *gorping* onto the pushing action, those who heard "the bunny and the duck are *gorping*" mapped *gorping* onto the arm movement acted by both characters. That is, the number of noun phrases and their positions relative to the verb, constrained infants' interpretation of a verb meaning (see Lee & Naigles, 2005, 2008, for evidence in Mandarin Chinese; Göksun, Küntay, & Naigles, 2008, for evidence in Turkish). More recent studies have further shown that two-year-olds can infer aspects of a novel verb's meaning from syntactic information on its own, in the absence of any visual input (Arunachalam & Waxman, 2010; Yuan & Fisher, 2009). Hearing a sentence such as "the duck is *gorping* the bunny" may be sufficient for toddlers to infer the causative structure of the action *gorping*. Likewise, four-year-old children tend to assign a cognitive meaning (e.g., to believe, to think) to a verb taking a sentence as complement ("The girl *gorps* that the boy is cute"; Papafragou et al., 2007). Syntactic structure can thus determine the interpretation of a novel verb by orienting infants' attention toward the relevant, physical or abstract, component of an event.

Syntactic bootstrapping phenomena show that word-meaning association is first constrained by the verb argument structure, a property in no way related to the perceptual and sensorimotor features of the associated meaning. Although certain syntactic structures (e.g., unergative intransitive frames: "the boy is *blicking*") might drive infants' attention toward the motor program of the implied action, infants tend to privilege the causal over the physical dimension (e.g., the manner of action), when the frame allows choosing between two interpretations (i.e., transitive frame). In a study by Bunger and Lidz (submitted for publication), two-year-old infants saw a scene depicting a novel action (e.g., a boy pumps a bike pump attached to a garden flower, causing the flower to spin) and heard a sentence including a novel verb to describe the action ("The boy is *blicking* the flower"). The authors reported that infants readily extended the same verb to a scene showing novel means (e.g., the boy makes the flower spin by hitting it with the hand) or results (e.g., the boy makes the flower move up and down by pumping), but not to a scene including the same means and results, but lacking causal relation (e.g., the boy pumps and the flower spins, but the pump is *not* connected to the flower). In other words, infants expected a transitive verb to express a causal relation between a motor act and a result, and attributed greater importance to this relation than to the motor act in itself, which became *optional* for the verb meaning.

The infant studies reviewed here suggest that verb learning does not work as a blind associationist mechanism, where word forms encode perceptual and motor dimensions of actions. Notions such as causality and intentionality seem to be weighted heavily in infants' perception and encoding of action, and possibly pre-exist lexical and motor developments (Carey, 2009; Meltzoff, 2007). Verb learning builds on these abstract representations. Moreover, the interpretation of a novel verb is largely guided by syntactic information: transitive constructions typically used to describe causative actions cue the encoding of an abstract causal relation, instead of the motor program to perform it. The idea that sensorimotor information is one core attribute of action meanings may be warranted in certain limited cases where the syntactic frame (e.g., ergative verbs), or pragmatic or perceptual factors focus infants' attention onto the action means; however, the encoding of sensory and motor features cannot account for the whole pattern of results describing how infants acquire verb meanings.

While conceptual and language representations are not exhausted by sensorimotor information, it is certain that the sensorimotor systems are involved in language and conceptual processes. In the following discussion, we will draft possible interpretations of this phenomenon.

5. Discussion

The literature reviewed here shows that linguistic and non-linguistic representations of actions rely on functionally distinct neural substrates, and that acquiring the meaning of words denoting motor events (i.e., verbs) is a complex process that brings together conceptual and syntactic information, beyond the perceptual and sensorimotor information related to the physical characteristics of the event. The mechanisms for language acquisition and the correlates of language disturbance show that sensorimotor information cannot be regarded as essential, or even central, to action-word understanding. A theory that wants to posit an important role for the sensorimotor system in conceptual tasks needs to integrate neuroimaging evidence for language-induced motor activity in *normal* language understanding with the neuropsychological evidence for independent action and language representations and with evidence for the dominance of conceptual and syntactic constraints over sensorimotor features in infants' word learning.

One possible way to approach such a theory is to establish the circumstances in which sensorimotor representations are elicited in normal language processing. Conceptual representations are retrieved automatically when people process words, regardless of the task (Neely, 1991; Stroop, 1935). If sensorimotor information is a substantial part of the lexical-semantic representation of an action word, sensorimotor areas should be activated automatically. Initial reports of language-induced motor activation appeared to support this prediction (Pulvermüller, 2005). However, later investigations on the phenomenon of language-induced sensorimotor activity have revealed that this activity is less ubiquitous than predicted in the embodied account of semantics. A number of studies showed that motor activity in response to action words was the most likely in those conditions in which the task demand required participants to attend the motor content of that word. For instance, using TMS to the left M1, Papeo et al. (2009) found increased motor activity for action (vs. nonaction) verbs, when participants had to perform semantic judgments (i.e., deciding whether an item was an action-related or a state verb), but not when they had to count the number of syllables in the same verbs (for other task-related effects, see Tomasino et al., 2007, 2008; Willems, Hagoort, et al. 2010; Willems, Toni et al., 2010). Consistently, greater motor and premotor BOLD signal was obtained when the linguistic context emphasized the motor meaning of an action verb (*kick the ball*), relative to when the context assigned the same action verb to a nonmotor meaning (i.e., in the idiomatic sentence: *kick the bucket*; Raposo et al., 2009; see also Rüschemeyer et al., 2007; but see Boulenger et al., 2009). Context-dependent modulation of sensorimotor activity was tested presenting action verbs in negative (vs. affirmative) sentences for semantic-sensibility judgments (Tomasino, Weiss, & Fink, 2010), or in negative sentences for silent reading (Tettamanti et al., 2008). In the "negative" conditions, sensorimotor regions were found to be significantly less activated compared with the condition were the same verbs were used in affirmative utterances. Finally, in a recent TMS study, Papeo et al. (2011) demonstrated that the very same action verbs elicited significantly greater motor facilitation when presented in first-person sentences (*afferro, I grasp*), than when presented in third-person sentences (*afferra, he grasps*). Importantly, even though the same action meaning applied to both the first- and the third-person items, the latter did not elicit greater facilitation as compared with (first- and third-person) nonaction verbs (i.e., the control condition).

This set of results suggests that the motor activity is not entirely stimulus-driven and does not respond automatically to the word's action content itself; the recruitment of the sensorimotor system in language understanding is instead modulated by the reliance on top-down factors, such as the individuals' attention to certain aspects of the stimuli, the task demand and the overall linguistic context in which a word is encountered. This *cognitive* mediation of the context is not predicted – and cannot be accounted – by a direct and automatic mechanism matching between a perceived action stimulus and the corresponding sensorimotor representation. This perspective accommodates observations from neuropsychology and developmental studies, as well as the neuroimaging results as reviewed here, which include evidence for language-related sensorimotor activity, but further inspect the conditions under which this phenomenon takes place. On this view, there is no conflict between neuropsychology and infant studies on the one hand, and neuroimaging and TMS studies on the other hand, but a convergence toward the conclusion that sensorimotor information is not necessary component of the conceptual representations of action.

Building on the consideration that action and language, interactive though they might be, are independent systems, researchers have proposed that the rehearsal of previous sensorimotor experience, resulting in sensorimotor activations, could provide a shortcut to the concrete attributes of a word meaning, when these are relevant to solve a task (Martin & Chao, 2001; Rumiati, Papeo, & Corradi-Dell'Acqua, 2010; Tranel, Damasio, & Damasio, 1997). The information flow between the sensorimotor and the conceptual domain may provide concepts with a physical instantiation that "colors" a word meaning and enriches comprehension (Mahon & Caramazza, 2008; Willems & Hagoort, 2007).

This view admits that, among the numerous, complex aspects forming action knowledge (e.g., the motor program, effector, typical context, typical agent, typical goal, intention, desires), some semantically relevant information could be carried by sensorimotor structures. Patients' ability to recognize an action-word is often tested in an "all-or-none" manner: either they recognize (or name) a word or they do not, either they recognize an action or they do not. Thus, one might wonder whether patients with motor dysfunction, who can still comprehend the meaning of an action-word, have in effect lost some aspects of that meaning; in other words, whether the way in which an apraxic represent an action meaning is "less colorful" than the way neurotypical individuals do. Such a difference would not be surprising, just like it is not that an expert dancer encodes a ballet differently than a neophyte (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; for a discussion, see Chatterjee, 2010).

Our argument can earn strength from analogy with observations in the domain of numerical cognition. The comprehension of number words in adults relies on at least two systems: a symbolic one that supports exact calculation and higher mathematics, and an approximate non-symbolic one, common to human adults (Dehaene & Cohen, 1997), infants (Xu & Spelke, 2000), neonates (Izard, Sann, Spelke, & Streri, 2009), and non-human species (Brannon & Terrace, 1998; Hauser, Carey, & Hauser, 2000). The approximate system yields magnitude representations that are analogically related to their referents; in the same way, a sensorimotor representation can be related to an actual action. Interestingly, Lemer, Dehaene, Spelke, and Cohen (2003) reported two neuropsychological patients showing a double dissociation between these two "number systems". One patient was impaired in approximate computations (e.g., subtraction), but was able to perform exact calculations and to retrieve rote knowledge about numbers. In other words, this patient possessed relatively intact knowledge of numbers and their properties as symbols, but exhibited impaired grounding of such symbols in the analogical *number sense* (Dehaene, 1997). The second patient showed the opposite behavior: he had intact approximation abilities and preserved processing of non-symbolic numerosities, but was impaired in tasks treating numbers as symbols (e.g., multiplication). Building on this analogy, a future line of research may investigate the extent to which the grounding of knowledge about actions (and action words) is impaired in an apraxic patient, while more abstract propositional knowledge is preserved.

Our suggestion that sensorimotor activation is not necessary for action-word understanding is largely orthogonal to the question of whether there exist neural substrates for mirror matching in humans. In this regard, we can imagine three possible scenarios. First, it could be argued that the mirror neurons found in monkeys, simply do not exist in humans. In this rather extreme view, mirror neurons in the macaque brain could code a primitive form of action representation that supports abstraction away from sensorimotor experience and generalization across entities, and in humans this might have been replaced by other, more specialized, structures (e.g., anterior temporal lobes; Patterson, Nestor, & Rogers, 2007). This hypothesis would be based on failure to find consistent evidence for the existence of humans' neurons that respond to action observation and execution using the fMRI cross-modal adaptation paradigm (see Lingnau et al., 2009). However, this hypothesis would require explaining what evolutionary constraints would have led to the disappearance of the mirror neuron system in humans. The investigation of monkey mirror neurons indeed suggests a functional relevance of this neural population that should have been favored instead of suppressed by evolution.

A second possibility is that mirror neurons exist in the human brain, in areas analog to those where the monkey mirror neurons have been found, but that they play no role in action understanding in either species. As Hickok (2009) observed, "*it is entirely possible that "mirror" responses are nothing more than the facilitation of the motor system via learned associations* [between a perceptual action-stimulus and a response]" (p. 1233; see also Tkach, Reimer, & Hatsopoulos, 2007). Notice that, as in the case of humans, there is no evidence in monkey studies that lesions to mirror neurons impair the capacity to recognize an action. Moreover, some results might be interpreted as an indication that the mirror activity in monkeys does not serve understanding through the rehearsal of individual motor experience: monkey mirror neurons could *learn* to respond to tool-use actions after 2-months of visual training, even though the monkey remained unable to manipulate those tools (Ferrari, Rozzi, & Fogassi, 2005).

A third hypothesis is that mirror neurons exist in humans, and are indeed used as a primitive system to understand others' actions when those actions are part of the observer's repertoire, and no other code is available. In particular, infants may use this system in the first months of their life to recognize in others' actions the goals and desires that they themselves have experienced (Meltzoff, 2007). While newborns may possess an abstract notion of "goal", they might not be able to recognize a goal in others' actions; a mirror mechanism might thus allow them to map this concept, initially associated with their own actions, to others' actions. This learning mechanism might then become obsolete and optional once higher level systems, including language, have matured to encode actions.

6. Conclusions

With this review, we have tried to assess the weight of sensorimotor representations in understanding action words. To shed new light on the current vivacious debate on the embodiment of concepts, we aimed to review the critical combination of information from different fields of research and different approaches to the study of human cognition. Taking advantage of the tradition of cognitive neuropsychology studies on language and praxis abilities, we argue that the system for action performance is functionally independent of conceptual system. A parallel conclusion is derived from the literature on infant studies. This line of research can provide unique insights into the basic and necessary pieces of information upon which the complex knowledge housed in an adult brain is built. Already in infants, sensorimotor properties do not appear to be privileged when representing actions, but give way to conceptual dimensions such as goals and intentions. In particular, verb learning seems to rely on conceptual and syntactic constraints, more than on the association of speech labels with physical acts. Available empirical results do not justify the conclusion that sensorimotor processes play a central role in learning and understanding action-words. This *fact* opens to crucial questions such as the extent to which the sensorimotor processes may contribute to solving the problem of symbol grounding (e.g., how meanings are realized in the specific context in which they appear) and/or serve as a primary mechanism in social cognition, to learn about others' goals and intentions.

Acknowledgments

The present research was supported by the Marie Curie International Outgoing Fellowship for Career Development called "Actico–Action in Concepts" awarded to LP and by the Marie Curie International Outgoing Fellowship for Career Development called "COIN – Compositionality in Infants" awarded to JRH. The authors are grateful to Raffaella I. Rumiati and to Amy Skerry for valuable comments on an earlier version of the manuscript.

References

Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In S. K. Newman, & R. Epstein (Eds.), *Current perspectives in dysphasia* (pp. 32–60). Edinburgh: Churchill Livingstone.

Anderson, S. E., Chiu, E., Huette, S., & Spivey, M. J. (2011). On the temporal dynamics of language-mediated vision and vision-mediated language. *Acta Psychologica*, *137*, 181–189.

Arévalo, A. L., Baldo, J. V., & Dronkers, N. F. (2010). What do brain lesions tell us about theories of embodied semantics and the human mirror neuron system? *Cortex*, http://dx.doi.org/10.1016/j.cortex.2010.06.001

Arévalo, A., Perani, D., Cappa, S., Butler, A., Bates, E., & Dronkers, N. (2007). Action and object processing in aphasia: From nouns and verbs to the effect of manipulability. *Brain and Language*, *100*, 79–94.

Arunachalam, S., & Waxman, S. R. (2010). Meaning from syntax: Evidence from 2-year-olds. *Cognition*, *114*(3), 442–446.

Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology*, *16*, 1818–1823.

Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with phonological changes in Brodmann areas 44 and 45 in the motor neurone disease-dementia-aphasia syndrome. *Brain*, *124*, 103–120.

Bak, T. H., Yancopoulou, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermüller, F., et al. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, *129*, 321–332.

Ball, W. A. (1973). *The perception of causality in the infant*. Paper presented at the meeting of the Society for Research in Child Development, March 29–April 1, Philadelphia, PA.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*, 577–660.

Barsalou, L. W. (2009). Simulation, situated conceptualization, and prediction. *Philosophical Transactions of the Royal Society of London Series B*, *364*, 1281–1289.

Bates, E., & Dick, F. (2002). Language, gestures, and the developing brain. *Developmental Psychobiology*, *40*, 293–310.

Bell, B. D. (1994). Pantomime recognition impairment in aphasia: An analysis of error types. *Brain and Language*, *47*, 269–278.

Bernal, S., Lidz, J., Millote, S., & Christophe, A. (2007). Syntax constrains the acquisition of verb meaning. *Language Learning and Development*, *3*, 325–341.

Borghi, A. M., Gianelli, C., & Scorolli, C. (2010). Sentence comprehension: Effectors and goals, self and others. An overview of experiments and implications for robotics. (Special topic edited by Angelo Cangelosi, *Action and language integration in cognitive systems*). *Frontiers in Neurorobotics*, http://dx.doi.org/10.3389/fnbot.2010.00003

Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cerebral Cortex*, *18*, 1905–1914.

Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. *Science*, *282*, 746–749.

Brune, C. W., & Woodward, A. L. (2007). Social cognition and social responsiveness in 10-month-old infants. *Journal of Cognition and Development*, *8*, 133–158.

Bunger, A., & Lidz, L. (2004). Syntactic bootstrapping and the internal structure of causative events. In *Proceedings of 28th Boston University conference on language development* (pp. 74–85). Cambridge: Cascadilla Press.

Bunger, A., & Lidz, J. Linguistic and conceptual constraints on verb learning, under revision.

Calvo-Merino, B., Glaser, D. E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: An fMRI study with expert dancers. *Cerebral Cortex*, *15*, 1243–1249.

Caramazza, A. (1986). On drawing inferences about the structure of normal cognitive systems from the analysis of patterns of impaired performance: The case for single-patient studies. *Brain and Cognition*, *5*, 41–66.

Caramazza, A., & Hillis, A. E. (1991). Lexical organization of nouns and verbs in the brain. *Nature*, *349*, 788–790.

Caramazza, A., Hillis, A. E., Rapp, B. C., & Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology*, *7*, 161–189.

Caramazza, A., & Shelton, J. R. (1998). Domain specific knowledge systems in the brain: The animate–inanimate distinction. *Journal of Cognitive Neuroscience*, *10*, 1–34.

Carey, S. (2009). *The origin of concepts*. New York: Oxford University Press.

Carey, S., & Bartlett, E. (1978). Acquiring a single new word. *Papers and Reports on Child Language Development*, *15*, 17–29.

Carey, S., & Spelke, E. S. (1994). Domain specific knowledge and conceptual change. In L. Hirschfeld, & S. Gelman (Eds.), *Mapping the mind: Domain specificity in cognition and culture* (pp. 169–200). Cambridge: Cambridge University Press.

Chao, L. L., & Martin, A. (1999). Cortical representation of perception, naming, and knowledge of color. *The Journal of Cognitive Neuroscience*, *11*, 25–35.

Chatterjee, A. (2010). Disembodying cognition. *Language and Cognition*, *2*, 79–116.

Chong, T. T.-J., Cunnington, R., Williams, M. A., Kanwisher, N., & Mattingley, J. B. (2008). fMRI adaptation reveals mirror neurons in human inferior parietal cortex. *Current Biology*, *18*, 1576–1580.

Chrisley, R., & Ziemke, T. (2002). Embodiment. In *Encyclopedia of cognitive science*. Macmillan.

Cotelli, M., Borroni, B., Manenti, R., Alberici, A., Calabria, M., Agosti, C., et al. (2006). Action and object naming in frontotemporal dementia, progressive supranuclear palsy, and coticobasal degeneration. *Neuropsychology*, *20*, 558–565.

Crepaldi, D., Berlingeri, M., Paulesu, E., & Luzzatti, C. (2011). A place for nouns and a place for verbs? A critical review of neurocognitive data on grammatical-class effects. *Brain and Language*, *116*, 33–49.

Csibra, G. (2008). Goal attribution to inanimate agents by 6.5-month-old infants. *Cognition*, *107*, 705–717.

Cubelli, R., Marchetti, C., Boscolo, G., & Della Sala, S. (2000). Cognition in action: Testing a model of limb apraxia. *Brain and Cognition*, *44*, 144–165.

Damasio, A., & Tranel, D. (1993). Nouns and verbs are retrieved with differentially distributed neural systems. *Proceedings of the National Academy of Science of the United States of America*, *90*, 4957–4960.

Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition*, *92*, 179–229.

Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C., & Gainotti, G. (1994). Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. *Neuropsychologia*, *32*, 1325–1341.

Daniloff, J. K., Noll, J. D., Fristoe, M., & Lloyd, L. L. (1982). Gesture recognition in patients with aphasia. *Journal of Speech and Hearing Disorders*, *47*, 43–49.

Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., et al. (1997). Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, *120*, 1763–1777.

Dee, H. L., Benton, A. L., & Van Allen, M. W. (1970). Apraxia in relation to hemispheric locus of lesion and aphasia. *Transactions of the American Neurological Association*, *95*, 147–150.

Dehaene, S. (1997). *The number sense*. New York: Oxford University Press.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantities knowledge of arithmetic. *Cortex*, *33*, 219–250.

De Renzi, E., Motti, F., & Nichelli, P. (1980). Imitating gestures: A quantitative approach to ideomotor apraxia. *Archives of Neurology*, *37*, 6–10.

De Renzi, E., Pieczuro, A., & Vignolo, L. A. (1968). Ideational apraxia: A quantitative study. *Neuropsychologia*, *6*, 41–52.

Devlin, J., Gonnerman, L., Andersen, E., & Seidenberg, M. (1998). Category-specific semantic deficits in focal and widespread brain damage: A computational account. *Journal of Cognitive Neuroscience*, *10*, 77–94.

Dinstein, I., Thomas, C., Behrmann, M., & Heeger, D. J. (2008). A mirror up to nature. *Current Biology*, *18*, R13–R18.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

Duffy, R. J., & Duffy, J. R. (1981). Three studies of deficits in pantomimic expression and pantomime recognition in aphasia. *Journal of Speech and Hearing Research*, *46*, 70–84.

Duffy, R. J., Duffy, J. R., & Pearson, K. L. (1975). Pantomime recognition in aphasics. *Journal of Speech and Hearing Research*, *18*, 115–132.

Feldman, J., & Narayanan, S. (2004). Embodied meaning in a neural theory of language. *Brain and Language*, *89*, 385–392.

Ferrari, P. F., Rozzi, S., & Fogassi, L. (2005). Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *Journal of Cognitive Neuroscience*, *17*, 212–226.

Ferro, J. M., Santos, M. E., Castro-caldas, A., & Mariano, G. (1980). Gesture recognition in aphasia. *Journal of Clinical and Experimental Psychology*, *2*, 277–292.

Finkelnburg, D. C. (1870). Niederrheinische Gesellschaft in Bonn, Sitzung vom 21. März 1870. *Berliner Klinische Wochenschrift*, *7*, 449–450, 460–462.

Fisher, C. (1996). Structural limits on verb mapping: The role of analogy in children's interpretations of sentences. *Cognitive Psychology*, *31*, 41–81.

Fisher, C. (2002). Structural limits on verb mapping: The role of abstract structure in 2.5-year-olds' interpretations of novel verbs. *Developmental Science*, *5*, 56–65.

Fisher, C., Gertner, Y., Scott, R., & Yuan, S. (2010). Syntactic bootstrapping. *Wiley Interdisciplinary Reviews: Cognitive Science*, *1*, 143–149.

Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: A review of the role of the motor system in language comprehension. *Quarterly Journal of Experimental Psychology*, *61*, 825–850.

Forbes, J. N., & Poulin-Dubois, D. (1997). Representational change in young children's understanding of familiar verb meaning. *Journal of Child Language*, *24*, 389–406.

Forbes, J. N., & Farrar, M. J. (1993). Children's initial assumptions about the meaning of novel motion verbs: Biased and conservative? *Cognitive Development*, *8*, 273–290.

Fodor, J. A. (1975). *The language of thought*. Cambridge, MA: Harvard University Press.

Fodor, J. A. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.

Gainotti, G., Caltagirone, C., Masullo, C., & Miceli, G. (1980). Patterns of neuropsychological impairment in various diagnostic groups of dementia. In L. Amaducci, A. N. Davison, & P. Antuono (Eds.), *Aging of the brain and dementia* (pp. 245–250). Raven Press: New York.

Gainotti, G., & Lemmo, M. S. (1976). Comprehension of symbolic gestures in aphasia. *Brain and Language*, *3*, 451–460.

Gentilucci, M., & Gangitano, M. (1998). Influence of automatic word reading on motor control. *European Journal of Neuroscience*, *10*, 752–756.

Gergely, G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature*, *415*, 755.

Gergely, G., Chen, M. L., & Király, I. (2011). *Opacity and relevance in social cultural learning: Relevance-guided emulation in 14-month-olds*. Talk given at the 2011 SRCD Biennial Meeting, Montreal, Canada.

Gergely, G., & Csibra, G. (2003). Teleological reasoning in infancy: The naive theory of rational action. *Trends in Cognitive Sciences*, *7*, 287–292.

Gergely, G., Nádasdy, Z., Csibra, G., & Bíró, S. (1995). Taking the intentional stance at 12 months of age. *Cognition*, *56*, 165–193.

Gillette, J., Gleitman, H., Gleitman, L. R., & Lederer, A. (1999). Human simulations of vocabulary learning. *Cognition*, *73*, 135–176.

Gleitman, L. R. (1990). The structural sources of verb meanings. *Language Acquisition*, *1*, 3–55.

Gleitman, L. R. (1994). Words, words, words. . .. *Philosophical Transactions of the Royal Society of London Series B*, *346*, 71–77.

Gleitman, L. R., & Gleitman, H. (1992). A picture is worth a thousand words, but that's the problem: The role of syntax in vocabulary acquisition. *Current Directions in Psychological Science*, *1*, 31–35.

Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin and Review*, *9*, 558–565.

Glenberg, A. M., Sato, M., Cattaneo, L., Riggio, L., Palumbo, D., & Buccino, G. (2008). Processing abstract language modulates motor system activity. *Quarterly Journal of Experimental Psychology*, *61*, 905–919.

Geschwind, N. (1965). Disconnexion syndromes in animals and man. *Brain*, *88*, 237–294.

Goldenberg, G., Hartmann, K., & Schlott, I. (2003). Defective pantomime of object use in left brain damage: Apraxia or asymbolia? *Neuropsychologia*, *41*, 1565–1573.

Goldstein, K. (1948). *Language and language disturbances: Aphasic symptom complexes and their significance for medicine and theory of language*. New York: Grune & Stratton.

Golinkoff, R. M., Church Jacquet, R., Hirsh-Pasek, K., & Nandakumar, R. (1996). Lexical principles may underlie the learning of verbs. *Child Development*, *67*, 3101–3119.

Golinkoff, R. M., & Hirsh-Pasek, K. (2008). How toddlers begin to learn verbs. *Trends in Cognitive Sciences*, *12*, 397–403.

Golinkoff, R. M., Hirsh-Pasek, K., Bailey, L. M., & Wenger, N. R. (1992). Young children and adults use lexical principles to learn new nouns. *Developmental Psychology*, *28*, 99–108.

Golinkoff, R. M., Hirsh-Pasek, K., Mervis, C. B., Frawley, W., & Parillo, M. (1995). Lexical principles can be extended to the acquisition of verbs. In M. Tomasello, & W. Merriman (Eds.), *Beyond names for things: Young children's acquisition of verbs* (pp. 185–223). Hillsdale, NJ: Erlbaum.

Göksun, T., Küntay, A., & Naigles, L. (2008). Turkish children use morphosyntax in extending verb meaning. *Journal of Child Language*, *35*, 291–323.

Goodglass, H., & Kaplan, E. (1963). Disturbance of gesture and pantomime in aphasia. *Brain*, *86*, 703–720.

Grabowski, T. J., Damasio, H., & Damasio, A. R. (1998). Premotor and prefrontal correlates of category-related lexical retrieval. *NeuroImage*, *7*, 232–243.

Halberda, J. (2003). The development of a word-learning strategy. *Cognition*, *87*, B23–B34.

Hachinski, V. (2002). Stroke: The next 30 years. *Stroke*, *33*, 1–4.

Hagoort, P. (2005). On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, *9*, 416–423.

Hartmann, K., Goldenberg, G., Daumüller, M., & Hermsdörfer, J. (2005). It takes the whole brain to make a cup of coffee: The neuropsychology of naturalistic actions involving technical devices. *Neuropsychologia*, *43*, 625–637.

Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor premotor cortex. *Neuron*, *41*, 301–307.

Hauser, M. D., Carey, S., & Hauser, L. B. (2000). Spontaneous number representation in semi-free-ranging rhesus monkeys. *Proceedings of the Royal Society of London, B: Biological Sciences*, *267*, 829–833.

Head, H. (1926). *Aphasia and kindred disorders of speech*. Cambridge: Cambridge University Press.

Hecaen, H. (1962). The clinical symptomatology of right and left hemispheric lesions. *Les Cahiers du Collège de Medecine des Hôpitaux de Paris*, *3*, 259–270.

Heibeck, T. H., & Markman, E. M. (1987). Word learning in children: An examination of fast mapping. *Child Development*, *58*, 1021–1034.

Hickok, G. (2009). Eight problems for the mirror neuron theory of action understanding in monkeys and humans. *Journal of Cognitive Neuroscience*, *21*, 1229–1243.

Hickok, G. (2010). The role of mirror neurons in speech perception and action word semantics. *Language and Cognitive Processes*, *25*, 749–776.

Hillis, A. E., Heidler-Gray, J., Newhart, M., Chang, S., Ken, L., & Bak, T. H. (2006). Naming and comprehension in primary progressive aphasia: The influence of grammatical word class. *Apasiology*, *20*, 246–256.

Hochmann, J. -R. Frequency, function words and the second Gavagai problem. *Cognition*, under revision.

Hochmann, J.-R., Endress, A. D., & Mehler, J. (2010). Word frequency as a cue to identify function words in infancy. *Cognition*, *115*, 444–457.

Hohenstein, J. M., Eisenberg, A., & Naigles, L. (2006). Is he floating across or crossing afloat? Cross-influence of La and L2 in Spanish–English bilingual adults. *Bilingualism: Language and Cognition*, *9*, 249–261.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526L 8.

Izard, V., Sann, C., Spelke, E. S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 10382–10385.

Jakobson, R. (1941/1968). *Child language, aphasia and phonological universals*. The Hague: Mouton.

Kamewari, K., Kato, M., Kanda, T., Ishiguro, H., & Hiraki, K. (2005). Six-and-a-half-month-old children positively attribute goals to human action and to humanoid-robot motion. *Cognitive Development*, *20*, 303–320.

Kemmerer, D., & Gonzalez Castillo, J. (2010). The two-level theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. *Brain and Language*, *112*, 54–76.

Kemmerer, D., Rudrauf, D., Manzel, K., & Tranel, D. Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex*, in press.

Kertesz, A., Ferro, J. M., & Shewan, C. M. (1984). Apraxia and aphasia: The functional-anatomical basis for their dissociation. *Neurology*, *34*, 40–47.

Kertesz, A., & Hooper, P. (1982). Praxis and language: The extent and variety of apraxia in aphasia. *Neuropsychologia*, *20*, 275–286.

Kintsch, W. (1998). The representation of knowledge in minds and machines. *International Journal of Psychology*, *33*, 411–420.
Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*, 846–848.
Koski, L., Wohlschlager, A., Bekkering, H., Woods, R. P., Dubeau, M-C., Mazziotta, J., et al. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex*, *12*, 847–855.
Kosugi, D., Ishida, H., & Fujita, K. (2003). 10-month-old infants' inference of invisible agent: Distinction in causality between object motion and human action. *Japanese Psychological Research*, *45*, 15–24.
Lakoff, G., & Johnson, M. (1980). *Metaphors we live by*. Chicago: University of Chicago Press.
Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh*. New York: Basic Books.
Lakusta, L., & Landau, B. (2005). Starting at the end: The importance of goals in spatial language. *Cognition*, *96*, 1–33.
Landau, B., & Gleitman, L. R. (1985). *Language and experience: Evidence from the blind child*. Cambridge, MA: Harvard University Press.
Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review*, *104*, 211–240.
Lee, J., & Naigles, L. R. (2005). Input to verb learning in mandarin Chinese: A role for syntactic bootstrapping. *Developmental Psychology*, *41*
Lee, J., & Naigles, L. (2008). Mandarin learners use syntactic bootstrapping in verb acquisition. *Cognition*, *106*, 1028–1037.
Lemer, C., Dehaene, S., Spelke, E. S., & Cohen, L. (2003). Approximate quantities and exact number words: Dissociable systems. *Neuropsychologia*, *41*, 1942–1958.
Lenneberg, E. H. (1967). *Biological foundations of language*. New York: Wiley.
Leslie, A. M. (1982). The perception of causality in infants. *Perception*, *11*, 173–186.
Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review*, *74*, 431–461.
Liepmann, H. (1905). Die linke Hemisphere und das Handeln. *Münchener Medzinische Wochenschrift*, *49*, 2322–2326, 2375–2378.
Lingnau, A., Gesierich, B., & Caramazza, A. (2009). Asymmetric fMRI adaptation reveals o evidence for mirror neurons in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 9925–9930.
Lock, A. (1980). *The guided reinvention of language*. London: Academic Press.
Longe, O., Randall, B., Stamatakis, E. A., & Tyler, L. K. (2007). Grammatical categories in the brain: The role of morphological structure. *Cerebral Cortex*, *17*, 1812–1820.
Mahon, B. Z., & Caramazza, A. (2005). The orchestration of the sensory-motor systems: Clues from neuropsychology. *Cognitive Neuropsychology*, *22*, 480–494.
Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis & a new proposal for grounding conceptual content. *Journal of Physiology – Paris*, *102*, 59–70.
Mahon, B. Z., & Caramazza, A. (2009). Concepts and categories: A cognitive neuropsychological perspective. *Annual Review of Psychology*, *60*, 27–51.
Mahon, B. Z., Milleville, S. C., Negri, G. A. L., Rumiati, R. I., Caramazza, A., & Martin, A. (2007). Action-related properties of objects shape object representations in the ventral stream. *Neuron*, *55*, 507–520.
Markman, E. M. (1990). Constraints children place on word meanings. *Cognitive Science*, *14*.
Markman, E. M., Wasow, J. L., & Hansen, M. B. (2003). Use of the mutual exclusivity assumption by young word learners. *Cognitive Psychology*, *47*, 241–275.
Markman, E. M., & Hutchinson, J. E. (1984). Children's sensitivity to constraints on word meaning: Taxonomic vs. thematic relations. *Cognitive Psychology*, *16*, 1–27.
Martin, A. (2007). Neural foundations for conceptual representations: Evidence from functional brain imaging. In J. Hart, & M. Kraut (Eds.), *The neural basis of semantic memory* (pp. 302–330). Cambridge University Press.
Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinions in Neurobiology*, *11*, 194–201.
Mätzig, S., Druks, J., Masterson, J., & Vigliocco, G. (2009). Noun and verb differences in picture naming: Past studies and new evidence. *Cortex*, *45*, 738–758.
McCarthy, R., & Warrington, E. K. (1985). Category specificity in an agrammatic patient: The relative impairment of verb retrieval and comprehension. *Neuropsychologia*, *23*, 709–727.
McClelland, J. L., & Rogers, T. T. (2003). The parallel distributed processing approach to semantic cognition. *Nature Reviews Neuroscience*, *4*, 310–322.
McShane, J. (1979). The development of naming. *Linguistics*, *17*, 879–905.
Meltzoff, A. N. (2007). 'Like me': A foundation for social cognition. *Developmental Science*, *10*, 126–134.
Mengotti, P., Negri, G. A. L., Corradi-Dell'Acqua, C., Trincia, E., Zadini, A., & Rumiati, R. I. (2009). Mapping language and action in the brain: Evidence from aphasia and apraxia. In *47th Annual Meeting of the Academy of Aphasia* Boston, October 18th–20th, 2009.
Merriman, W. E., Evey-Burkey, J. A., Marazita, J. M., & Jarvis, L. H. (1996). Young two-year-olds' tendency to map novel verbs onto novel actions. *Journal of Experimental Child Psychology*, *63*, 466–498.
Mervis, G. B. (1987). Child-basic object categories and early lexical development. In U. Neisser (Ed.), *Concepts and conceptual development: Ecological and intellectual factors in categorization* (pp. 201–233). Cambridge: Cambridge University Press.
Miceli, G., Silveri, M. C., Nocentini, U., & Caramazza, A. (1988). Patterns of dissociation in comprehension and production of nouns and verbs. *Aphasiology*, *2*, 251–258.
Mozaz, M., Rothi, L. J., Anderson, J. M., Crucian, G. P., & Heilman, K. M. (2002). Postural knowledge of transitive pantomimes and intransitive gestures. *Journal of the International Neuropsychological Society*, *8*, 958–962.
Muentener, P., & Carey, S. (2006). What is the domain of causal perception? Investigating causal perception of motion and non-motion state change events in infancy. *Journal of Vision*, *6*, 965.
Naigles, L. (1990). Children use syntax to learn verb meanings. *Journal of Child Language*, *17*, 357–374.
Naigles, L. G., & Kako, E. T. (1993). First contact in verb acquisition: Defining a role for syntax. *Child Development*, *64*, 1665–1687.
Naigles, L., & Terrazas, P. (1998). Motion verb generalizations in English and Spanish: Influences of language and syntax. *Psychological Science*, *9*, 363–369.
Neary, D., Snowdon, J. S., Mann, D. M., Northen, B., Goulding, P. J., & Macdermott, N. (1990). Frontal lobe dementia and motor neuron disease. *Journal of Neurology, Neurosurgery and Psychiatry*, *53*, 23–32.
Neely, J. H. (1991). Semantic priming effects in visual word recognition: A selective review of current findings and theories. In D. Besner, & G. W. Humphreys (Eds.), *Basic processes in reading* (pp. 264–336). Hillsdale, NJ: Lawrence Erlbaum Associates.
Negri, G. A. L., Rumiati, R. I., Zadini, A., Ukmar, M., Mahon, B. Z., & Caramazza, A. (2007). What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cognitive Neuropsychology*, *24*, 795–816.
Ochipa, C., Rothi, L. J., & Heilman, K. M. (1989). Ideational apraxia: A deficit in tool selection and use. *Annals of Neurology*, *25*, 190–193.
Oliveri, M., Finocchiaro, C., Shapiro, K., Gangitano, M., Caramazza, A., & Pascual-Leone, A. (2004). All talk and no action: A transcranial magnetic stimulation study of motor cortex activation during action word production. *Journal of Cognitive Neuroscience*, *16*, 347–381.
Papafragou, A., Cassidy, K., & Gleitman, L. (2007). When we think about thinking: The acquisition of belief verbs. *Cognition*, *105*, 125–165.
Papafragou, A., & Selimis, S. (2010). Event categorization and language: A cross-linguistic study of motion. *Language and Cognitive Processes*, *25*, 224–260.
Papagno, C., Della Sala, S., & Basso, A. (1993). Ideomotor apraxia without aphasia and aphasia without apraxia: The anatomical support for a double dissociation. *Journal of Neurology, Neurosurgery and Psychiatry*, *56*, 286–289.
Papeo, L., Negri, G. A. L., Zadini, A., & Rumiati, R. I. (2010). Action performance and action-word understanding: Evidence of double dissociations in left-damaged patients. *Cognitive Neuropsychology*, *27*, 428–461.
Papeo, L., Corradi-Dell'Acqua, C., & Rumiati, R. I. (2011). She is not like I: The tie between language and action is in our imagination. *The Journal of Cognitive Neuroscience*, *23*, 3939–3948.
Papeo, L., Vallesi, A., Isaja, A., & Rumiati, R. I. (2009). Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS ONE*, *4*, e4508.
Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*, 976–987.
Pauen, S., & Träuble, B. (2009). How 7-month-olds interpret ambiguous motion events: Category-based reasoning in infancy. *Cognitive Psychology*, *59*, 275–295.
Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011a). Bridging the gap between the other and me: The functional role of motor resonance and action effects in infants' imitation. *Developmental Science*, *14*, 901–910.
Paulus, M., Hunnius, S., Vissers, M., & Bekkering, H. (2011b). Imitation in infancy: Rational or motor resonance? *Child Development*, *82*, 1047–1057.
Pfeifer, R., & Scheier, C. (1999). *Understanding Intelligence*. Cambridge, MA: MIT Press.
Petrides, M., & Pandya, D. N. (1994). Comparative architectonic analysis of the human and the macaque frontal cortex. In F. Boller, & J. Grafman (Eds.), *Handbook of neuropsychology* (pp. 17–58). Amsterdam: Elsevier.
Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, *9*, 129–154.
Pruden, S. M., & Hirsh-Pasek, K. (2006). Foundations of verb learning: Labels promote action category formation. In D. Bamman, T. Magnitskaia, & C. Zaller (Eds.), *Proceedings of the 30th Annual Boston University Conference on Language Development* (pp. 467–477). Somerville, MA: Cascallida Press.
Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, *6*, 576–582.
Pulvermüller, F., & Fadiga, L. (2010). Active perception: Sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, *11*, 351–360.
Pulverman, R., & Golinkoff, R. M. (2004). Seven-month-olds' attention to potential verb referents in nonlinguistic events. In A. Brugos, L. Micciulla, & C. E. Smith (Eds.), *Proceedings of the 28th Annual Boston University Conference on Language Development* (pp. 473–480). Somerville, MA: Cascallida Press.
Pylyshyn, Z. W. (1984). *Computation and cognition: Toward a foundation for cognitive science*. Cambridge, MA: MIT/Bradford.
Rapcsak, S. Z., Ochipa, C., Anderson, K. C., & Poizner, H. (1995). Progressive ideomotor apraxia: Evidence for a selective impairment in the action production system. *Brain and Cognition*, *27*, 213–236.
Raposo, A., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2009). Modulation of motor and premotor cortices by actions, action words and action sentences. *Neuropsychologia*, *47*, 388–396.
Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*, 169–192.
Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*, 131–141.
Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–670.

Rosci, C., Valentina, C., Laiacona, M., & Capitani, E. (2003). Apraxia is not associated to a disproportionate naming impairment for manipulable objects. *Brain and Cognition*, *53*, 412–415.
Rothi, L. J. G., Ochipa, C., & Heilman, K. M. (1991). A cognitive neuropsychological model of limb praxis. *Cognitive Neuropsychology*, *8*, 443–458.
Rumiati, R. I., Papeo, L., & Corradi-Dell'Acqua, C. (2010). Higher-level motor processes. *Annals of the New York Academy of Science*, *1191*, 219–241.
Rumiati, R. I., Zanini, S., Vorano, L., & Shallice, T. (2001). A form of ideational apraxia as a selective deficit of contention scheduling. *Cognitive Neuropsychology*, *18*, 617–642. http://www.informaworld.com/smpp/title~db=all~content=t713659042~tab=issueslist~branches=18-v18
Rüschemeyer, S. A., Brass, M., & Friederici, A. D. (2007). Comprehending prehending: neural correlates of processing verbs with motor stems. *Journal of Cognitive Neuroscience*, *19*, 855–865.
Saygin, A. P., Wilson, S. M., Dronkers, N. F., & Bates, E. (2004). Action comprehension in aphasia: Linguistic and non-linguistic deficits and their lesion correlates. *Neuropsychologia*, *42*, 1788–1804.
Saxe, R., Tenenbaum, J., & Carey, S. (2005). Secret agents: 10 and 12-month-olds infer an unseen cause of the motion of an inanimate object. *Psychological Science*, *16*, 995–1001.
Saxe, R., Tzelnic, T., & Carey, S. (2007). Knowing who-dunnit: Infants identify the causal agent in an unseen causal interaction. *Developmental Psychology*, *43*, 149–158.
Scheerer, E. (1984). Motor theories of cognitive structure: A historical review. In W. Prinz, & A. F. Sanders (Eds.), *Cognition and motor processes* (pp. 77–98). Berlin: Springer-Verlag.
Shallice, T. (1988). *From neuropsychology to mental structure*. Cambridge: Cambridge University Press.
Siegel, L. S. (1981). Infant tests as predictors of cognitive and language development at two years. *Child Development*, *52*, 545–557.
Siri, S., Tettamanti, M., Cappa, S. F., Della Rosa, P., Saccuman, C., Scifo, P., et al. (2008). The neural substrate of naming events: Effects of processing demands but not of grammatical class. *Cerebral Cortex*, *18*, 171–177.
Soja, N., Carey, S., & Spelke, E. (1985). *Constraints on word learning*. Paper presented at the 1985 Biennial Convention of the Society for Research in Child Development, Toronto, Canada.
Sommerville, J. A., & Woodward, A. L. (2005). Infants' sensitivity to the causal features of means-end support relations in action and perception. *Infancy*, *8*, 119–145.
Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, *96*, B1–B11.
Southgate, V., Johnson, M. H., & Csibra, G. (2008). Infants attribute goals to even biologically impossible actions. *Cognition*, *107*, 1059–1069.
Spelke, E. S., Phillips, A., & Woodward, A. L. (1995). Infants' knowledge of object motion and human action. In D. Sperber, D. Premack, & A. Premack (Eds.), *Causal cognition: A multidisciplinary debate* (pp. 44–78). Oxford, UK: Clarendon Press.
Stager, C. L., & Werker, J. F. (1997). Infants listen for more phonetic detail in speech perception than in word learning tasks. *Nature*, *388*, 381–382.
Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.
Tkach, D., Reimer, J., & Hatsopoulos, N. G. (2007). Congruent activity during action and action observation in motor cortex. *Journal of Neuroscience*, *27*, 13241–13250.
Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*, 273–281.
Tettamanti, M., Manenti, R., Della Rosa, P. A., Falini, A., Perani, D., Cappa, S. F., et al. (2008). Negation in the brain: Modulating action representations. *NeuroImage*, *43*, 358–367.
Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Science of the United States of America*, *94*, 14792–14797.
Tomasino, B., Fink, G. R., Sparing, R., Dafotakis, M., & Weiss, P. H. (2008). Action verbs and the primary motor cortex: A comparative TMS study of silent reading, frequency judgments, and motor imagery. *Neuropsychologia*, *46*, 1915–1926.
Tomasino, B., Weiss, P. H., & Fink, G. R. (2010). To move or not to move: Imperatives modulate action-related verb processing in the motor system. *Neuroscience*, *169*, 246–258.
Tomasino, B., Werner, C. J., Weiss, P. H., & Fink, G. R. (2007). Stimulus properties matter more than perspective: An fMRI study of mental imagery and silent reading of action phrases. *NeuroImage*, *36*, 128–141.
Tranel, D., Damasio, H., & Damasio, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, *35*, 1319–1327.
Tucker, M., & Ellis, R. (2004). Action priming by briefly presented objects. *Acta Psychologica*, *116*, 185–203.
Turella, L., Pierno, A. C., Tubaldi, F., & Castiello, U. (2009). Mirror neurons in humans: Consisting or confounding evidence? *Brain and Language*, *108*, 10–21.
Tyler, L. K., Bright, P., Fletcher, P., & Stamatakis, E. A. (2004). Neural processing of nouns and verbs: The role of inflectional morphology. *Neuropsychologia*, *42*(4), 512–523.
Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, *5*, 244–252.
Varney, N. R. (1978). Linguistic correlates of pantomime recognition in aphasic patients. *Journal of Neurology, Neurosurgery and Psychiatry*, *41*, 564–568.
Vigliocco, G., Warren, J., Siri, S., Arciuli, J., Scott, S., & Wise, R. (2006). The role of semantics and grammatical class in the neural representation of words. *Cerebral Cortex*, *16*, 1790–1796.
Wang, L., & Goodglass, H. (1992). Pantomime, praxis, and aphasia. *Brain and Language*, *42*, 402–418.
Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, *106*, 859–878.
Warrington, E. K., & McCarthy, R. A. (1987). Categories of knowledge: Further fractionations and an attempted integration. *Brain*, *110*, 1273–1296.
Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairment. *Brain*, *107*, 829–854.
Watson, J. B. (1913). Psychology as the behaviorist views it. *Psychological Review*, *20*, 158–177.
Werker, J. F., Cohen, L. B., Lloyd, V. L., Casasola, M., & Stager, C. L. (1998). Acquisition of word-object associations by 14-month-old infants. *Developmental Psychology*, *34*, 1289–1309.
Wernicke, C. (1874). *The aphasic symptom-complex. A psychological study on an anatomical basis*. Breslau, Germany: Cohn and Weigert. [Translated from German].
Willems, R. M., & Hagoort, P. (2007). Neural evidence for the interplay between language, gesture, and action: A review. *Brain and Language*, *101*, 278–289.
Willems, R. M., Hagoort, P., & Casasanto, D. (2010). Body-specific representations of action verbs: Neural evidence from right- and left-handers. *Psychological Science*, *21*, 67–74.
Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2010). Neural dissociations between action verbs understanding and motor imagery. *Journal of Cognitive Neuroscience*, *22*, 2387–2400.
Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *9*, 625–636.
Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition*, *69*, 1–34.
Woodward, A. L. (1999). Infants' ability to distinguish between purposeful and non-purposeful behaviors. *Infant Behavior and Development*, *22*, 145–160.
Woodward, A. L. (2009). Infants' grasp of others' intentions. *Current Directions in Psychological Science*, *18*, 53–57.
Woodward, A. L., & Guajardo, J. J. (2002). Infants' understanding of the point gesture as an object-directed action. *Cognitive Development*, *17*, 1061–1084.
Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition*, *74*, B1–B11.
Yuan, S., & Fisher, C. (2009). Really? She blicked the baby? Two-year-olds learn combinatorial facts about verbs by listening. *Psychological Science*, *20*, 619–626.
Zacks, J. M., & Tversky, B. (2001). Event structure in perception and cognition. *Psychological Bulletin*, *127*, 3–21.
Zwaan, R. A. (2004). The immersed experiencer: Toward an embodied theory of language comprehension. In B. H. Ross (Ed.), *The psychology of learning and motivation* (pp. 35–62). Academic Press: New York.
Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: Motor resonance in language comprehension. *Journal of Experimental Psychology General*, *135*, 1–11.