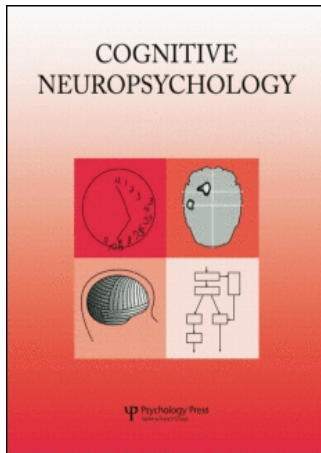


This article was downloaded by:[Ingenta Content Distribution]
On: 29 November 2007
Access Details: [subscription number 768420433]
Publisher: Psychology Press
Informa Ltd Registered in England and Wales Registered Number: 1072954
Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Cognitive Neuropsychology

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title~content=t713659042>

The orchestration of the sensory-motor systems: Clues from Neuropsychology

Bradford Z. Mahon; Alfonso Caramazza

Online Publication Date: 01 May 2005

To cite this Article: Mahon, Bradford Z. and Caramazza, Alfonso (2005) 'The orchestration of the sensory-motor systems: Clues from Neuropsychology', *Cognitive Neuropsychology*, 22:3, 480 - 494

To link to this article: DOI: 10.1080/02643290442000446

URL: <http://dx.doi.org/10.1080/02643290442000446>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

THE ORCHESTRATION OF THE SENSORY-MOTOR SYSTEMS: CLUES FROM NEUROPSYCHOLOGY

Bradford Z. Mahon and Alfonso Caramazza

Harvard University, Cambridge, USA

Research over the last several decades has led to clear and empirically tractable proposals about the representation of conceptual knowledge in the brain. Here we argue that there are already sufficient data from neuropsychology to strongly constrain extant hypotheses about the representation of conceptual knowledge. One constraint imposed by these neuropsychological data is that recognition of actions and understanding of objects do not necessarily depend on the ability to produce object-associated actions. This conclusion compels a reconsideration of the role played by motor planning and/or execution processes in action and object recognition and understanding.

INTRODUCTION

As the articles in this Special Issue of *Cognitive Neuropsychology* attest, the role of the sensory-motor systems in higher cognitive functions is a hot topic in the cognitive brain sciences. Convergence of the methods of cognitive neuropsychology, functional imaging, and behavioural work with normal subjects has led to clear hypotheses about the roles of sensory-motor processes and structures in higher-order cognitive processes. Such roles range from inferring and/or understanding the intentions and emotions of conspecifics (Adolphs, 2003; Blakemore & Decety, 2001; Gallese & Goldman, 1998) to the principles that determine the organisation and representation of conceptual knowledge of concrete objects and actions (Allport, 1985; Barsalou, Simmons, Barbey, & Wilson, 2003; Gallese & Lakoff, 2005; Martin, Ungerleider, & Haxby, 2000; Warrington & McCarthy, 1983, 1987; Warrington & Shallice,

1984). In this article, we focus on the role of the sensory-motor systems in representing conceptual knowledge of concrete objects and actions.

One way to organise theories of the representation of conceptual knowledge is to distinguish so-called “embodied” from “disembodied” theories (e.g., Fadiga & Craighero, 2003; Feldman & Narayanan, 2003; Garbarini & Adenzato, 2004; Lakoff & Johnson, 1999). Embodied theories of conceptual representation argue that conceptual content is reducible (i.e., really *is*) sensory-motor content (e.g., Barsalou et al., 2003; Lakoff & Johnson, 1999; Pulvermuller, 2001); disembodied theories of conceptual representation argue that the information/processes internal to the sensory-motor system are not sufficient to exhaust what we know about concrete object and action concepts (e.g., Caramazza, Hillis, Rapp, & Romani, 1990; Humphreys & Forde, 2001; Plaut, 2002; Tyler & Moss, 2001; Warrington & McCarthy, 1987). The notion of simulation, or

Correspondence should be addressed to Alfonso Caramazza, Department of Psychology, William James Hall, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA (Email: Caram@wjh.harvard.edu).

Preparation of this manuscript was supported in part by NIH grant DC04542 to AC, and by an NSF Graduate Research Fellowship to BZM. We are grateful to Jorge Almeida, Leslie Gonzalez-Rothi, Raffaella Rumiati, Kyle Simmons, and Naomi Zack for comments on an earlier version of this manuscript.

the reactivation of sensory-motor information in the course of conceptual processing, is required by embodied but not by disembodied theories of concept representation.

We discuss two aspects of the hypothesis of embodied conceptual knowledge: (1) the role of motor production processes in the recognition of visually presented actions; and (2) the role of motor production processes in the representation of conceptual knowledge of objects and actions. The discussion is organised in this way because there are varying degrees of strength at which the hypothesis of embodied conceptual knowledge may be developed. We take as the immediate stimulus for our discussion of these important issues the recent article by Gallese and Lakoff (2005 this issue), in which the authors defend a particularly strong version of the embodied hypothesis. For instance, while previous authors (e.g., Barsalou et al., 2003) have argued for a central role of sensory-motor content in representing conceptual knowledge of objects and actions, Gallese and Lakoff argue for the stronger position that integrative processes within the sensory-motor system obviate the need to postulate such processes outside the sensory-motor system.¹

We undertake this project because we believe that there are already sufficient neuropsychological data to constrain hypotheses about the role of motor production processes in the recognition and understanding of objects and actions. At present, the available neuropsychological data may not be sufficiently rich as to adjudicate at a fine-grained level between specific implementations of the embodied and disembodied hypotheses. However, we believe that there is already sufficient neuropsychological evidence to define the boundaries of empirically viable theories of the representation of conceptual knowledge.

ACTION RECOGNITION

Research over the last several decades has produced a rich array of empirical demonstrations of neural activation of sensory-motor structures that is not specific to a given modality of input or output. Much of what is known comes from single-cell recordings in macaque monkeys (for reviews, see, e.g., Fadiga & Craighero, 2003; Rizzolatti, Fogassi, & Gallese, 2001); more recently, functional imaging techniques have permitted analogous questions to be addressed to the human brain (e.g., Bremner et al., 2001; Buccino et al., 2001; Hari, Forss, Avikainen, Kirveskari, Salenius, & Rizzolatti, 1998; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Martin, Wiggs, Ungerleider, & Haxby, 1996; Tettamanti et al., 2005; for reviews, see Grèzes, & Decety, 2001; Martin & Chao, 2001). Behavioural work with human subjects has also implicated motor planning and/or execution processes in the recognition of sensory input (e.g., Edwards, Humphreys, & Castiello, 2003; Shiffrar & Freyd, 1990; Viviani & Stucchi, 1989).

One phenomenon central to the hypothesis of embodied cognition is the behaviour of mirror neurons: neurons that are activated both during motor execution as well as during action observation (e.g., Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). The types of visual input that are sufficient to activate mirror neurons are highly constrained, for instance by the types of motor movements for which the neurons also fire. Recent work has also shown that some mirror neurons in macaque premotor cortex are activated by both visual and auditory input (Kohler, Keysers, Umiltà, Fogassi, Gallese, & Rizzolatti, 2002).

¹ "To claim, as we do, that an action like *grasping* is multimodal is to say that (1) it is neurally enacted using neural substrates used for both action and perception, and (2) that the modalities of action and perception are integrated at the level of the sensory-motor system itself and not via higher association areas" (p. 459, emphasis original). Gallese and Lakoff (2005) situate these proposals in a broader theory of human cognition that treats a wide range of issues, from the principles that guide praxis, to the architecture of the sensory-motor system, to whether human cognition is mediated by symbols. We will not discuss the issues of imagination, parameters, metaphor, structured neural computation, nor the implications of their basic assumptions for a theory of language (for recent discussion of the available hypothesis space on the latter issue, see Fitch, Hauser, & Chomsky, in press; Pinker & Jackendoff, 2005).

One way in which such phenomena (e.g., mirror neuron activation) have been interpreted within the embodied cognition framework is that motor production processes and structures are necessarily involved in the recognition of visually presented actions. We will refer to this proposal as the “Motor Theory of Action Recognition,” after a closely related theory of speech perception (Lieberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967): The claim made by the Motor Theory of Speech Perception was that in order to recognise speech sounds, it was necessary for the listener to run or simulate the corresponding motor programs that would result in the production of the same sounds.

Broadly speaking, there are two levels of strength at which the Motor Theory of Action Recognition can be formulated, roughly corresponding to two ways in which the behaviour of (e.g.) mirror neurons might be interpreted. The weaker interpretation is that motor processes/structures *respond* to visual or auditory input. In this sense, the process is multimodal not (necessarily) in terms of the perceptual content that is represented, but in terms of the types of perceptual content (perhaps represented elsewhere) that trigger the process. A stronger interpretation that may be given to the claim that a process is multimodal is that sensory content or sensory properties of a given type (e.g., auditory) are represented in motor cortex (or the cortex formerly known as motor). Recent discussion of these issues has emphasised that hypotheses about the nature of the mapping from perceptual input to motor output representations lie along a continuum (Rumiati & Bekkering, 2003).

Gallese and Lakoff (2005) advance a strong interpretation of the behaviour of mirror neurons, in proposing that “[c]ortical pre-motor areas are endowed with sensory properties” (p. 459), and that “... circuitry across brain regions links modalities, infusing each with properties of others” (p. 456). This strong interpretation is consistent with the authors’ broader theoretical commitments about the structure of the mind/brain: namely, that all of the integration required by higher cognitive functions occurs inside the sensory-motor system.² Here we focus on one central empirical commitment of the Motor Theory of Action Recognition, which can be reduced to either of two hypotheses:

Hypothesis I: Recognition of action is mediated by processes required to produce action, and, at least at the level required for successful recognition of actions, recognition and production processes are not functionally separable.

Hypothesis II: At the levels of representation required for successful recognition and production of actions, recognition and production are functionally separable; however, evaluation of the perceptual input requires simulation of the corresponding motor output routines.³

One way to evaluate the Motor Theory of Action Recognition is to consider the performance of patients with apraxia, an impairment in using objects that cannot be attributed to aphasia, sensory impairment, or an impairment to basic motor responses. Both Hypotheses I and II generate the prediction that apraxia will necessarily be associated with an inability to correctly recognise visually presented actions. Contrary to this

² It is sometimes not clear if Gallese and Lakoff (2005) are arguing *for* multimodality or *against* modularity. These authors distinguish their use of the term “multimodality” from “supramodality”: “This is important theoretically because supramodality is consistent with the idea of strict modularity, while multimodality is not. Supramodality accords with a picture of the brain containing separate modules for action and for perception that need to be somehow ‘associated.’ *Multimodality denies the existence of such separate modules*” (p. 459, emphasis original). The claim that “[m]ulti-modality denies the existence of... modules” (p. 459) does not accord with all construals of either multimodality or modularity. In the way modularity was originally proposed (Fodor, 1983), it was not a property of cognitive processes that distinguished (either empirically, or a priori) between modality-specific and multimodal systems. One could, by hypothesis, have modular multimodal processes; perhaps the process(es) underlying the McGurk effect illustrate(s) one such example (Fodor, 1983; Footnote 13 therein).

³ For instance, it might be argued that selection of the “correct” interpretation of perceptual input is guided by motor planning and/or execution programs (e.g., Viviani & Stucchi, 1992).

prediction is the performance of a number of patients who are impaired at using objects but who are not impaired at distinguishing correct from incorrect object-associated actions (Bartolo, Cubelli, Della Sala, Drei, & Marchetti, 2001; Bergego, Pradat-Diehl, & Deloche, 1992; Dumont & Ska, 2000; Dumont, Ska, Schiavetto, 1999; Halsband, Schmitt, Weyers, Binkofski, Grützner, & Freund, 2001; Mozaz, Rothi, Anderson, Crucian, & Heilman, 2002; Ochipa, Rothi, & Heilman, 1989; Rapcsak, Ochipa, Anderson, & Poizner, 1995; Rumiati, Zanini, Vorano, & Shallice, 2001; Schwartz, Montgomery, Fitzpatrick-DeSalme, Ochipa, Coslett, & Mayer, 1995).

For instance, Rumiati and colleagues (2001) report two apraxic patients, DR and FG, neither of whom presented with visual agnosia for objects or for pantomimes.⁴ Patients DR and FG were impaired at demonstrating the correct actions associated with the use of objects, both for single object use (DR: 16/28; FG: 18/28) and for multiple object use (DR: 4/10; FG: 2/10; data from session IV). However, the ability of both patients to sequence photographs of actions in the correct order (9/10 both patients; session IV) and to recognise the correct actions associated with objects (DR: 15/15; FG 14/15) was preserved. Of particular interest is the fact that patient FG was 95% correct (19/20) at discriminating correct from incorrect actions when the incorrect actions were reproductions of actual errors that FG had made in a previous testing session.

The majority of FG's errors were "conceptual errors," or movements that were kinematically fluent but were (for instance) not appropriate to the object at hand, or were applied to the incorrect part of the object. Thus, it might be argued that the impairment in FG is actually "more abstract" than the level at which action recognition processes are

mediated by action production processes. However, the same pattern observed in FG is observed in patients who make predominantly kinematic (or production) errors. One clear and carefully studied case, GW (Rapcsak et al., 1995), was not able to produce any correct pantomimes of object use (to 15 stimuli) across a range of input modalities: visual presentation of objects, verbal command, and imitation. GW was also severely impaired at using actual objects correctly (1/15 right hand; 3/15 left hand). Spatio-temporal errors accounted for 90% of the patient's errors in action production, with the remaining 10% classified as body-part-as-object errors. Neither conceptually inappropriate actions nor perseverations were observed. Despite a prevalence of kinematic errors in action production, GW was flawless at naming object associated pantomimes (15/15), and was very good at discriminating correct from incorrect transitive pantomimes (14/15).

According to the Motor Theory of Action Recognition, the ability to recognise actions depends on the integrity of processes required to produce actions. The dissociation between action production and action recognition indicates that production processes are not required for correct recognition. Furthermore, it cannot be argued that recognition of actions is *merely* easier than production of actions, as the reverse impairment has also been observed. The pattern of impairment labelled "pantomime agnosia" (Rothi, Mack, & Heilman, 1986) consists of impaired recognition of the correct actions associated with the use of objects, but relatively unimpaired production of object-associated actions (Bell, 1994; Rothi et al., 1986, see Cubelli, Marchetti, Boscolo, & Della Salla, 2000, for a double dissociation between apraxia-without-pantomime-agnosia versus pantomime-agnosia-without-apraxia over the same materials).⁵

⁴ Where clarity of exposition requires, we will distinguish "transitive" from "intransitive" pantomimes. Following conventions in the literature "transitive pantomimes" are mimed actions that are associated with objects (e.g., hammering), whereas "intransitive pantomimes" are mimed actions that do not involve an object (e.g., waving goodbye).

⁵ Pantomime agnosia cannot be attributed to a "general" agnosia, for two reasons. First, patients with visual agnosia for objects do not necessarily present with pantomime agnosia (Schwartz, Barrett, Crucian, & Heilman, 1998); and second, the patient reported by Rothi and colleagues (1986) who was impaired at discriminating and identifying correct pantomimes, was not impaired at imitating pantomimes. The fact that the patient was not impaired at pantomime imitation indicates that the inability to identify actions cannot be due to a "general" visual impairment.

The observation of clear impairments to action production, but spared recognition of object-associated actions, is difficult to reconcile with certain construals of the Motor Theory of Action Recognition. Most obviously, it cannot be true that perception and production of actions are *completely* integrated at the level required for correct recognition. As discussed above, it is not entirely clear whether or not this was the intended claim of Gallese and Lakoff (2005).⁶ Second, these data indicate that even if perceptual and production processes are assumed to be functionally separate at the level required for correct recognition, the ability to produce correct actions is not necessary for successful recognition.

We have interpreted the Motor Theory of Action Recognition as assuming that the ability to produce learned object-associated actions is what supports successful recognition of visually presented actions. However, another way in which this theory could be developed would be to assume that what supports correct recognition of actions is a more basic ability to translate visual input to motor output. In other words, it might be argued that it is the ability to imitate that is required in order to recognise actions. There are, however, findings contrary to this development of the Motor Theory of Action Recognition. In a group study, Halsband and colleagues (2001) found that while patients with lesions to parietal areas were impaired at imitating visually presented actions, they were relatively unimpaired at recognising visually presented actions; importantly, there was no correlation between the ability to imitate gestures and the ability to recognise gestures. The pattern of dissociation observed by Halsband and colleagues in their group study has been corroborated by

single case studies as well. Recall that for both of the apraxic patients DR and FG (Rumiati et al., 2001) discussed above, recognition of actions was not impaired. However, while patient DR was classified as impaired for action imitation, FG was classified as performing within the normal range, indicating that the ability to imitate visually presented actions is not causally related to the ability to recognise actions. The same conclusion is compelled by the performance of patient BS (Bartolo et al., 2001; see also Goldenberg & Hagmann, 1997), who was in the normal range at recognising and identifying visually presented actions, pantomiming both transitive and intransitive actions to verbal, visual, and tactile input, as well as imitating both transitive and intransitive learned pantomimes. However, this patient was impaired (4/15) at imitating meaningless (i.e., unlearned) actions. It seems that what the patient has lost is the ability to translate arbitrary actions (presented visually) to motor output; such an ability would seem to be the most basic mechanism underlying simulation, and thus embodied recognition of actions. Given that recognition is not impaired in this patient, we can conclude that the ability to imitate actions is not required to successfully recognise actions.⁷

The empirical generalisations that emerge from this brief review of the neuropsychological evidence can be summarised as follows: (1) production of actions can be impaired while recognition of actions is spared; (2) recognition of actions can be impaired while production of actions is spared; and (3) imitation of meaningless actions can be impaired while recognition of actions is spared. These empirical facts have been summarised previously (Cubelli et al., 2000;

⁶ For example: "Multimodality does everything that supramodality has been hypothesised to do, and more. Multimodal integration has been found in many different locations in the brain, and we believe that it is the norm. . ." (Gallese & Lakoff, 2005, p. 459).

⁷ The fact that BS was unimpaired at imitating transitive and intransitive actions indicates that a general input deficit cannot explain the patient's inability to imitate meaningless gestures. Similarly, this deficit cannot be attributed to a production deficit, since the patient was not markedly impaired at producing transitive and intransitive gestures across a number of modalities of input. Following the model of praxis proposed by Rothi and colleagues (1991), the impairment in BS would be localised to the "sub-lexical" route for extracting motor information from visual input. This mechanism is similar to the orthography-phonology conversion mechanism postulated by many models of language processing, in that it is motivated by patients (e.g., BS) who are impaired at imitating meaningless gestures (cf. reading nonwords) but not meaningful or learned gestures (cf. reading real words).

Johnson-Frey, 2004; Rothi et al., 1991) and are consistent with models of praxis that draw a functional distinction between the representations that underlie perception and the representations that underlie production of actions (e.g., Cubelli et al., 2000; Rapcsak et al., 1995; Rothi et al., 1991; Rumiaty et al., 2001).⁸ Theories that assume that motor production processes are necessary to successfully recognise actions have difficulty accounting for these empirical facts.

UNDERSTANDING OBJECTS AND ACTIONS

A second aspect of the hypothesis of embodied cognition concerns the role of sensory-motor processes in higher cognitive functions such as language, theory of mind, and conceptual processing. Here we focus on the role of simulation over sensory-motor processes in the representation of object and action concepts, as we believe this issue is directly tractable from the perspective of extant neuropsychological data. The possible hypothesis space for the role of sensory-motor simulation in the representation of conceptual content spans a wide range: from no role at all to exhaustive, including a middle position in which

simulation adds to, but does not exhaust, the content of concrete object concepts.⁹ Again, we take as an impetus for our discussion the particularly strong hypothesis advanced by Gallese and Lakoff (2005, p. 456): “We will argue that conceptual knowledge is embodied, that is, it is mapped within our sensory-motor system. We will argue that the sensory-motor system not only provides structure to conceptual content, but also characterises the semantic content of concepts in terms of the way we function with our bodies in the world.”

This proposal can be distinguished from the Sensory/Motor Theory of Martin and colleagues (2000; see also Allport, 1985). The Sensory/Motor Theory argues that the organisation of the sensory-motor system drives the *organisation*, and perhaps in part underlies the representation, of conceptual knowledge of concrete objects and actions. The Sensory/Motor Theory does not assume that sensory-motor information/processes are sufficient to represent *all* that we know about concrete object and action concepts.¹⁰

Consider some of the empirical findings Gallese and Lakoff (2005) cite in support of their proposal.¹¹ Of particular importance are data from what have been referred to as “canonical neurons.” Single-cell recording studies in monkeys have revealed populations of neurons that fire

⁸ Nontrivial predictions can be extrapolated from these generalisations. For instance, recall the study on mirror neurons by Kohler and colleagues (2002). In that study, it was observed that a population of neurons responded both to the auditory and to the visual presentation of actions. The position which holds that recognition of actions is independent of production processes at the level required for successful recognition predicts that it should be possible to observe apraxic patients who are not impaired at recognising the correct sounds associated with those actions that they are not able to correctly produce.

⁹ This portrayal of the hypothesis space goes back to antiquity: “As to the nature and number of the first principles opinions differ. The difference is greatest between those who regard them as corporeal and those who regard them as incorporeal, and from both dissent those who make a blend and draw their principles from both sources. The number of principles is also in dispute; some admit one only, others assert several” (Aristotle, *De Anima*, 405a, 30–35).

¹⁰ In fact, Gallese and Lakoff (2005) advance the even stronger claim that the “inferential structure” of abstract concepts can also be reductively traced back to sensory-motor information/processes. Here we restrict our discussion to the representation of concrete concepts, on the assumption that if [sensory-motor content + simulation] is not sufficient to represent concrete object concepts, then [sensory-motor content + simulation + metaphor] will not be sufficient to represent abstract concepts.

¹¹ The arguments developed by Gallese and Lakoff (2005) assume that evidence for the existence of simulative processes is *ipso facto* evidence for the claim that such simulation grounds conceptual content. For instance: “According to our hypothesis, understanding requires simulation. The understanding of concrete concepts—physical actions, physical objects, and so on—requires sensory-motor simulation. But sensory-motor simulation, as suggested by contemporary neuroscience, is carried out by the sensory-motor system of the brain. It follows that the sensory motor system *is required for understanding at least concrete concepts*. We see this as an insurmountable difficulty for any traditional theory that claims that concrete concepts are modality-neutral and disembodied” (p. 468, emphasis original). We will take up in the final section ‘PULLING IT ALL TOGETHER’ the issue of whether demonstrations of simulative processes present an insurmountable difficulty for disembodied theories.

both when the monkey performs a goal-directed action on an object, and when the monkey sees the object (e.g., for review, see Rizzolatti et al., 2001). In humans, arguably comparable findings consist of the observation that ventral premotor cortex is more activated when subjects are presented with familiar tools than with equally familiar but not graspable objects (for review, see Martin & Chao, 2001). Gallese and Lakoff contend that “[t]he existence of canonical neurons and their putative equivalent in humans could underpin basic-level categories of objects,” and further, that “... *all* concrete concepts—concepts of things we can see, touch, and manipulate—can be addressed by [this] strategy...” (p. 469; emphasis original).¹² This is a particularly strong claim, and it generates predictions of the following form. In order to name a picture of a pair of scissors it is necessary to retrieve the motor programs associated with the use of scissors. Or, in order to judge that a pair of scissors is more similar to a knife than to a mallet in terms of function (function understood as what the object is used for), again, it is necessary to retrieve the motor information that allows correct utilisation of scissors, knives, and mallets.

The view assumed by Gallese and Lakoff (2005) is committed to the claim that there can be no understanding of concrete object concepts if the sensory-motor content over which such concepts are distributed is not present. Contrary to this hypothesis is the performance of apraxic patients who are not impaired for conceptual knowledge of graspable objects. There are a number of such patients (Buxbaum & Saffran, 2002; Buxbaum, Sirigu, Schwartz, & Klatzky, 2003; Buxbaum, Veramonti, & Schwartz, 2000; Cubelli et al., 2000; Halsband et al., 2001; Hodges, Spatt, & Patterson, 1999; Montomura

& Yamadori, 1994; Moreaud, Charnaliet, & Pellat, 1998; Ochipa et al., 1989; Rapcsak et al., 1995; Rosci, Valentina, Laiacona, & Capitani, 2003; Rumiati et al., 2001; for review, see Johnson-Frey, 2004; for discussion, see Dumont, Ska, & Joanette, 2000; Hodges, Bozeat, Lambon Ralph, Patterson, & Spatt, 2000; Mahon & Caramazza, 2003). For instance, Rosci and colleagues (2003) designed a study to specifically investigate the issue of whether impairments for object use are related to deficits in conceptual knowledge of manipulable objects. A group of 15 apraxic patients were administered: (1) a picture-naming test, (2) an auditory word-picture matching test, and (3) two tests of praxis performance (pantomime of object use to visual presentation of the object, and pantomime imitation). The stimuli used in the picture naming and auditory picture-word matching test consisted of 20 manipulable objects, 15 manmade but nonmanipulable objects, and 15 animals; the same 20 manipulable objects were used in the picture naming and word-picture matching test as were used in the object use test. The authors divided the patients into two groups twice: either in terms of whether or not they were impaired at imitation or in terms of whether or not they were impaired at pantomiming the use of objects. There was no indication of worse performance for manipulable objects compared to nonmanipulable objects in either the picture naming or the picture-word matching tasks. This was the case for: (1) patients who were impaired at imitation, (2) patients who were impaired at pantomiming the use of objects, and (3) patients who were impaired both at imitation and pantomiming the use of objects. Thus, neither a deficit for imitating visually presented actions nor a deficit for producing learned object-associated actions is

¹² Two types of simulative processes that Gallese and Lakoff (2005) take to bear equally on their proposal must be distinguished. Some types of simulative processes may be understood as being voluntary and/or explicit (e.g., mental imagery, mental rotation, etc.), while some types of simulative processes may be understood as being automatic and/or implicit (e.g., the behaviour of mirror neurons and canonical neurons). It is not at all clear that the evidence for voluntary simulation is relevant to a theory of the representation of conceptual knowledge. The reason is that such evidence does not bear on either of two claims, one of which must be intrinsic to the content-reductive hypothesis: (1) simulation over sensory-motor content exhausts conceptual content; (2) simulation over sensory-motor content is necessary for understanding concrete concepts.

necessarily associated with a disproportionate conceptual impairment for manipulable objects.

Individual case studies have confirmed the observations made by Rosci and colleagues (2003). For instance, patients FG and DR (Rumiati et al., 2001), discussed above, were perfect at identifying objects based on descriptions of the objects' function. This was the case even for the same objects on which the patients made apraxic errors. Similarly, both patients were perfect at matching objects to descriptions of the purpose or function of their appropriate actions (e.g., bar soap: to wash hands, to wash dishes, to wash the car; see also patient JK, Schwartz et al., 1995). Similarly, the apraxic patient GW (Rapcsak et al., 1995), discussed above, who was unimpaired at recognising transitive gestures despite an inability to produce such gestures without movement errors, was at ceiling on several tasks investigating the integrity of conceptual knowledge. For instance, this patient was at ceiling on tasks requiring a tool to be: (1) matched to its correct function, (2) selected from a set of alternatives in order to complete an unfinished task, as well as (3) selected as an alternative (i.e., noncanonical tool) to complete an unfinished task. GW was also unimpaired at providing verbal descriptions of: (1) the actions associated with objects, and (2) the functions of tools.

The empirical generalisation that emerges is that impairments in using objects correctly are not associated with impairments to conceptual knowledge of either objects or the functions of the actions associated with those objects.¹³ Previous reviews have arrived at this empirical generalisation (Cubelli et al., 2000; Hodges et al., 2000; Johnson-Frey, 2004; Rothi et al., 1991; Rumiati et al., 2001; for further discussion, see Mahon & Caramazza, 2003). From this fact, it follows that conceptual knowledge of concrete object and action concepts is not exhausted by simulation over sensory-motor content.

PULLING IT ALL TOGETHER

We have focused on two central aspects of the proposal that cognition is embodied. First, we discussed what we referred to as the Motor Theory of Action Recognition; this hypothesis holds that motor production processes and structures are necessarily implicated in the successful recognition of visually presented actions. Neuropsychological data were reviewed indicating that recognition of visually presented actions does not depend on either, (1) the ability to imitate visually presented actions, or (2) the ability to produce the correct actions associated with objects. Second, we discussed the hypothesis that the content of concrete object and action concepts can be reductively traced back through simulation to sensory-motor content. Neuropsychological data were reviewed, indicating that motor production processes are not required to support intact conceptual knowledge of manipulable objects or their associated actions.

We have chosen to focus on a rather narrow range of neuropsychological data in our review, but there are other neuropsychological phenomena that would also potentially bear on the embodied cognition hypothesis. For instance, similar to the double dissociation between apraxia-without-pantomime-agnosia versus pantomime-agnosia-without-apraxia is the dissociation between optic-ataxia-without-visual-form-agnosia versus visual-form-agnosia-without-optic-ataxia. Patients with optic ataxia are impaired at making visually guided prehension movements, but are spared for the motor movements involved in prehension as well as visually discriminating the relevant perceptual aspects of objects required for visually guided prehension (e.g., Jeannerod, Decety, & Michel, 1994; Milner et al., 2001). In contrast, visual form agnosics, such as patient DF, extensively studied by Goodale, Milner, and colleagues (e.g., Goodale, Milner, Jakobson, & Carey, 1991; Milner et al.,

¹³ This pattern constitutes one side of a double dissociation: The other side concerns patients who are impaired for conceptual knowledge of objects but relatively unimpaired at using objects correctly (e.g., Negri, Lunardelli, Gigli, & Rumiati, in press; Sirigu, Duhamel, & Poncet, 1991).

1991) are impaired at visually discriminating objects, but unimpaired at making visually guided prehension movements.

As outlined in the Introduction, strong versions of the embodied cognition hypothesis (e.g., Gallese & Lakoff, 2005) assume that all “higher-order cognitive processes” (e.g., conceptual processing, syntactic processing) reduce to sensory-motor processes. In other words, on the strong version of the embodied cognition hypothesis, simulation over sensory-motor content obviates the need to postulate “higher-order cognitive systems” in the first place (e.g., a conceptual system, a narrow language faculty). In contrast, disembodied theories assume that the information/processes internal to sensory-motor systems are not sufficient to represent such higher-order processes.

The evidence that is cited for the embodied hypothesis is not inconsistent with the disembodied hypothesis. For instance, Baldissera, Cavallari, Craighero, and Fadiga (2001) demonstrated modulation of spinal excitability during observation of hand actions in humans. Equally striking, Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) observed modulation of responses in hand muscles when subjects observed an agent grasping an object. In one sense, these data demonstrate that recognition and understanding really *are* embodied: The effects of observing grasping behaviour promulgates all the way to the hand. But this does not mean that the muscles in the hand play any role in recognition and/or understanding; these findings do not embarrass a view that holds that conceptual knowledge is functionally distinct from the processes subserved by spinal neurons and/or hand muscles. In other words, these data could just as readily be used to ground

a *reductio* argument against strong versions of the embodied cognition hypothesis (for discussion, see Oliveri, Finocchiaro, Shapiro, Gangitano, Caramazza, & Pascual-Leone, 2004). To the degree that one is not compelled to infer the necessity of muscle activation for conceptual understanding, why then make the inference that the activation of motor cortices is necessary for understanding? Or similarly, to the degree that one is not compelled to assume that muscle/spinal activation is sufficient to ground conceptual understanding, why then make the inference that motor information is sufficient to ground conceptual knowledge?

In contrast, the neuropsychological evidence we have reviewed is inconsistent with the embodied hypothesis but not with the disembodied hypothesis. The fact that apraxic patients are not necessarily impaired for conceptual knowledge of the same objects that they cannot correctly manipulate indicates that conceptual knowledge is not exhausted by motor information corresponding to the ways in which objects are manipulated (for further discussion, see Mahon & Caramazza, 2003). We believe that the neuropsychological approach is extremely useful in this regard, as it permits causal inferences to be drawn about the organisation and representation of cognitive processes.

The neuropsychological phenomena that we have reviewed compel a model that assumes the orchestration of “independent” perceptual and motor processes.¹⁴ By “independent”, we mean that at the relevant level of analysis, perceptual and motor processes are functionally separable. The “relevant level of analysis” is determined by the minimal computations that would be necessary in order to succeed in a given task, for instance

¹⁴ On the terminology of some authors (e.g., Gallese & Lakoff, 2005) any systems/processes that “orchestrate” sensory-motor systems are, by definition, “disembodied.” Furthermore, there seems to be some antipathy toward postulating cognitive processes that are in this sense disembodied, presumably because it is believed that disembodied cognitive processes are not tractable constructs from a biologically/neurologically oriented account of behaviour. It is not obvious what the weight of this charge might be; this use of the term “disembodied” seems to suggest cognitive processes that could not (in principle) be described as neural processes, or could not (in principle) exist “in the brain.” Another way to view these relations is that *no* cognitive processes are “in the brain” or “in the body,” in the way that, for instance, coffee is “in the cup” or the car is “in the garage.” Rather, mental processes *are* the functioning of the brain, in the sense that digestive processes *are* the functioning of the digestive system. We have adopted the embodied–disembodied terminology in order to facilitate connection of the issues discussed herein with those discussed by other authors.

recognition of pantomimes or production of pantomimes. In other words, we have argued that the assumption is compelled that perceptual and motor processes are “independent” *to the degree warranted* by the double dissociation between pantomime-agnosia-without-apraxia and apraxia-without-pantomime-agnosia. This does not imply, however, that multimodal integrative processes are not involved in, or do not affect, recognition of sensory input.

The situation is similar in regard to the inference that conceptual knowledge is not exhausted by information internal to the sensory-motor systems: This inference does not commit one to the assumption that simulation over sensory-motor content does not make important contributions to our conceptual knowledge of objects and actions (for discussion, see Caramazza & Mahon, *in press*). Consider, for instance, the recent and elegant study by Tettamanti and colleagues (2005), in which it was demonstrated that even just listening to simple sentences describing actions involving parts of the human body leads to activation of body-specific areas of motor planning structures. One way to interpret these data would be to assume that the activation of motor structures is necessary in order to understand verbs describing bodily actions. However, the data do not sanction this inference; much stronger data would be required in order to argue for the necessity of motor structures in conceptual understanding. Namely, it would have to be shown that, effectively removing such structures impairs the ability to understand verbs describing bodily actions. The data reported by Tettamanti and colleagues sanction the inference that such activation is an automatic consequence of exposure to the semantic content of actions describing bodily actions. This inference then opens up the issue of what the consequences of this automatic activation are, if any, for how we understand such verbs.

Even before the advent of technologies that permitted cognitive scientists to address questions to the brain, similar theoretical issues have been raised by behavioural work demonstrating interactions between distinct modalities. For instance,

Seidenberg and Tanenhaus (1979; Donnenwerth-Nolan, Tanenhaus, & Seidenberg, 1981) demonstrated an influence of orthographic similarity on rhyme judgments for auditorily presented words (see also Tanenhaus, Flanigan, & Seidenberg, 1980 for an analogous effect between visually presented primes and targets that are phonologically but not orthographically related; for recent review, see Muneaux & Ziegler, 2004). The basic finding reported by Seidenberg and Tanenhaus (1979) was that subjects are faster to decide that two words rhyme when they are orthographically similar (e.g., pie–tie) than when they are orthographically dissimilar (e.g., rye–tie). What is surprising about these data is that orthography has an influence *at all* on the decision process of whether two auditorily presented words rhyme. In this case, however, the implication is not that there is a representation in common between phonology and orthography; the reason why is that there is nothing in common between the motor movements involved in producing phonology and the motor movements involved in writing. Even if one were to ascend, as it were, to a more abstract level, it is not likely to be the case that a common, motor-relevant representation underlies phonological and orthographic information. Instead, one inference to be extracted from these data is that the auditory presentation of a word automatically leads to activation of its orthography, and that the *decision* process in a given task uses any information that is available for the execution of that task. In other words, the lack of a motor-relevant isomorphism between phonology and orthography blocks, as it were, the inference that simulation over orthographic representations is required in order to make rhyme judgments on auditory input.

In the case of human action recognition, however, there is a clearer isomorphism between the visual input and the motor output. As we have argued, the fact that motor production systems are engaged during recognition of actions does not imply that simulation is required for successful recognition and understanding. The neuropsychological evidence from apraxia

substantiates this argument. Thus, an isomorphism between perception and action *may* implicate a mechanism or representation common to perception and action, but it need not. Furthermore, even if it were assumed that the presence of an isomorphism between perception and action does implicate a common mechanism, it is an independent issue as to where in the cognitive architecture that shared representation is to be located.

One case of a clear isomorphism across perception and action is demonstrated by an elegant series of studies by Viviani and his collaborators. Lacquaniti, Terzuolo, and Viviani (1983) observed that the velocity of extemporaneous (i.e., unconstrained) hand movements at any point in a curvilinear planar trajectory is proportional to the cubic root of the instantaneous radius of curvature: as the radius of curvature decreases (i.e., the trajectory becomes more curved) the velocity decreases (this relation is referred to as the Two-Thirds Power Law). Thus, if subjects are asked to move their hand in a circle, the velocity of the movement is constant; if however, subjects are asked to move their hand in an elliptical path, the velocity of the movement is lowest at the poles and greatest in the flatter parts. Interestingly, if subjects are presented with a visual stimulus of a dot moving in the geometric trajectory of a circle, but following the velocity profile natural to manual elliptical motion, the stimulus is perceived to be flatter (i.e., more like an ellipse) than it actually is. Similarly, the perceived path of a dot moving in the geometric trajectory of a horizontal ellipse but following the velocity profile that would be natural to an ellipse rotated 90 degrees (i.e., a vertical ellipse) is rounder (i.e., more like a circle) than it actually is (Viviani & Stucchi, 1989, 1992). Subsequent work (Viviani, Baud-Bovy, & Redolfi, 1997) demonstrated that the identical illusion observed in the visual modality is also observed kinaesthetically when the hand is passively moved and subjects are blindfolded.

The work of Viviani and colleagues elegantly portrays a clear isomorphism; the Two-Thirds Power Law is observed to constrain in

qualitatively the same way both the interpretation of visual and kinaesthetic input as well as overt movements of the hands. This isomorphism between perception and action would seem, if anything would, to warrant an interpretation in terms of simulation. A simulationist perspective would place the Two-Thirds Power Law constraint internal to the motor system; for instance, it could be assumed that automatic activation of motor engrams constrains selection of perceptual input (e.g., Viviani & Stucchi, 1992). However, it is also clear that it is at least logically possible that the shared mechanism could be either (1) internal to the visual system, or (2) an amodal representation accessed by both the visual and the motor systems.

In a study of smooth pursuit eye movements, de'Sperati and Viviani (1997) demonstrated that, as is the case for hand movements, smooth pursuit eye movements are also constrained by the Two-Thirds Power Law. Given that movements of the hands and smooth pursuit movements of the eyes are subserved by separate neural and muscular systems, it becomes perhaps less likely that simulation over motor production processes are responsible for the perceptual illusions. Which motor production processes are simulated: those subserving smooth pursuit movements of the eyes or those subserving movements of the hands? As argued by Viviani and colleagues (de'Sperati & Viviani, 1997; Viviani et al., 1997) these data may suggest that the Two-Thirds Power Law exerts its influence on motor output, kinaesthetic input, and visual input at a more central, amodal level of representation.

Our intention here is not to argue for any specific locus in the cognitive architecture of the Two-Thirds Power Law constraint, but merely to make the following point: The presence of a strict isomorphism between perception and action does not, in and of itself, sanction the inference that simulation of motor processes underlies the perceptual phenomenon. To the degree that it is assumed that an isomorphism implies a shared mechanism, it remains an independent issue as to where in the cognitive architecture that shared mechanism is to be located.

Alternatively, there is the possibility that at the level(s) of representation sufficient to process the perceptual input and motor output correctly, perceptual and motor processes are functionally distinct. In other words, it could be the case that visual perception and motor production are subject to analytically identical, but functionally distinct, constraints.

Neuropsychological data play an important role in constraining embodied and disembodied theories of cognition. The neuropsychological approach is powerful because it can be used to establish causal inferences regarding the organisation and representation of cognitive processes. Of course, however, the neuropsychological approach, as all approaches, is not without its limitations. One potential limitation relevant to the issues discussed herein concerns the possibility that the ways in which the mind/brain successfully completes a given task under conditions of damage may involve processing steps that are not implicated as necessary processing steps under normal (i.e., undamaged) conditions. This possibility has important implications for determining the minimal computations (i.e., the relevant level(s) of analysis) that are necessarily required in order to successfully complete a given task. Notwithstanding such potential limitations (see Caramazza, 1992, for discussion), the neuropsychological approach, in concert with functional neuroimaging and neurophysiological methodologies, can support strong inferences about the principles that govern the organisation and representation of cognitive processes.

It has also been our intention to highlight the importance of the embodied cognition hypothesis and, in particular, the notion that simulation may play an important role in many cognitive processes. In one sense, perception must ultimately be *for* action, in that it is only action that allows an organism to interact, and ultimately survive and reproduce. The simulation hypothesis is a very important proposal, and is fruitfully pursued at first in its strongest form. Careful consideration of the strong version of the embodied cognition hypothesis opens up important questions. For instance, it is an open issue as to

what the role of simulation is in a theory of action recognition and understanding. Clearly, there is rich evidence from functional neuroimaging and neurophysiology suggesting that simulation plays an important role. Balancing the neuroimaging and neurophysiology data against the patterns of dissociation observed with the neuropsychological approach is, we believe, a profitable strategy towards understanding the role of simulation in the representation of conceptual knowledge.

PrEview proof published online 16 March 2005

REFERENCES

- Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. *Nature Reviews Neuroscience*, *4*, 165–178.
- Allport, D. A. (1985). Distributed memory, modular subsystems and dysphasia. In S.K. Newman & R. Epstein (Eds.), *Current perspectives in dysphasia*. New York: Churchill Livingstone.
- Aristotle. (1992). *Introduction to Aristotle* (Ed. by Richard McKeon). New York: The Modern Library.
- Baldissera, F., Cavallari, P., Craighero, L., & Fadiga, L. (2001). Modulation of spinal excitability during observation of hand actions in humans. *European Journal of Neuroscience*, *13*, 190–194.
- Barsalou, L. W., Simmons, W. K., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in the modality-specific systems. *Trends in Cognitive Sciences*, *7*, 84–91.
- Bartolo, A., Cubelli, R., Della Sala, S., Drei, S., & Marchetti, C. (2001). Double dissociation between meaningful and meaningless gesture reproduction in apraxia. *Cortex*, *37*, 696–699.
- Bell, B. D. (1994). Pantomime recognition impairment in aphasia: An analysis of error types. *Brain and Language*, *47*, 269–278.
- Bergego, C., Pradat-Diehl, P., & Deloche, G. (1992). Apraxie idéatoire et reconnaissance de l'utilisation des objets. *Revue de Neuropsychologie*, *2*, 193–206.
- Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*, *2*, 561–567.

- Bremner, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K.-P., Zilles, K., & Fink, G. R. (2001). Polymodal motion processing in posterior parietal and premotor cortex. A human fMRI study strongly implies equivalencies between humans and monkeys. *Neuron*, *29*, 287–296.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H. J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buxbaum, L. J., & Saffran, E. M. (2002). Knowledge of object manipulation and object function: Dissociations in apraxic and non-apraxic subjects. *Brain and Language*, *82*, 179–199.
- Buxbaum, L. J., Sirigu, A., Schwartz, M. F., & Klatzky, R. (2003). Cognitive representations of hand posture in ideomotor apraxia. *Neuropsychologia*, *41*, 1091–1113.
- Buxbaum, L. J., Veramonti, T., & Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: Knowing “what for” but not “how.” *Neurocase*, *6*, 83–97.
- Caramazza, A. (1992). Is cognitive neuropsychology possible? *Journal of Cognitive Neuroscience*, *4*, 80–95.
- Caramazza, A., Hillis, A. E., Rapp, B. C., & Romani, C. (1990). The multiple semantics hypothesis: Multiple confusions? *Cognitive Neuropsychology*, *7*, 161–189.
- Caramazza, A., & Mahon, B. Z. (in press). The organization of conceptual knowledge in the brain: The future’s past and some future directions. *Cognitive Neuropsychology*.
- 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.
- de’Sperati, C., & Viviani, P. (1997). The relationship between curvature and velocity in two-dimensional smooth pursuit eye movements. *Journal of Neuroscience*, *17*, 3932–3945.
- Donnenwerth-Nolan, S., Tanenhaus, M. K., & Seidenberg, M. S. (1981). Multiple code activation in word recognition: Evidence from rhyme monitoring. *Journal of Experimental Psychology: Human Learning and Memory*, *7*, 170–180.
- Dumont, C., & Ska, B. (2000). Pantomime recognition impairment in Alzheimer’s Disease. *Brain and Cognition*, *43*, 177–181.
- Dumont, C., Ska, B., & Joannette, Y. (2000). Conceptual apraxia and semantic memory deficit in Alzheimer’s disease: Two sides of the same coin? *Journal of International Neuropsychological Society*, *6*, 693–703.
- Dumont, C., Ska, B., & Schiavetto, A. (1999). Selective impairment of transitive gestures: An unusual case of apraxia. *Neurocase*, *5*, 447–458.
- Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain and Cognition*, *53*, 495–502.
- Fadiga L., & Craighero L., (2003). New insights on sensorimotor integration: From hand action to speech perception *Brain and Cognition*, *53*, 514–524.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Feldman, J., & Narayanan, S. (2003). Embodied meaning in a neural theory of language. *Brain and Language*, *89*, 385–392.
- Fitch, W. T., Hauser, M. D., & Chomsky, N. (in press). Evolution of the language faculty: Clarifications and implications. *Cognition*.
- Fodor, J. A. (1983). *The modularity of mind*. Cambridge MA: MIT Press.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind reading. *Trends in Cognitive Sciences*, *2*, 493–501.
- Gallese, V., & Lakoff, G. (2005). The brain’s concepts: The role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, *22*, 455–479.
- Garbarini, F., & Adenzato, M. (2004). At the root of embodied cognition: Cognitive science meets neurophysiology. *Brain and Cognition*, *56*, 100–106.
- Goldenberg, G., & Hagmann, S. (1997). The meaning of meaningless gestures: A study of visuo-imitative apraxia. *Neuropsychologia*, *35*, 333–341.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*, 154–156.
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19.

- Halsband, U., Schmitt, J., Weyers, M., Binkofski, F., Grützner, G., & Freund, H. J. (2001). Recognition and imitation of pantomimed motor acts after unilateral parietal and premotor lesions: A perspective on apraxia. *Neuropsychologia*, *39*, 200–216.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences*, *95*, 15061–15065.
- Hodges, J. R., Bozeat, S., Lambon Ralph, M. A., Patterson, K., & Spatt, J. (2000). The role of conceptual knowledge in object use. Evidence from semantic dementia. *Brain*, *123*, 1913–1925.
- Hodges, J. R., Spatt, J., & Patterson, K. (1999). “What” and “how”: Evidence for the dissociation of object knowledge and mechanical problem-solving skills in the human brain. *Proceedings of the National Academy of Sciences, USA*, *96*, 9444–9448.
- Humphreys, G. W., & Forde, E. M. (2001). Hierarchies, similarity, and interactivity in object recognition: “Category-specific” neuropsychological deficits. *Behavioural and Brain Sciences*, *24*, 453–509.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following bilateral posterior parietal lesion. *Neuropsychologia*, *32*, 369–380.
- Johnson-Frey, S.H. (2004). The neural basis of complex tool use in humans. *Trends in Cognitive Sciences*, *8*, 71–78.
- 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.
- Lacquaniti, F., Terzuolo, C., & Viviani, P. (1983). The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica*, *54*, 115–130.
- Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh*. New York: Basic Books.
- Liberman, A. M., Cooper, F. S., Shankweiler, D. P., & Studdert-Kennedy, M. (1967). Perception of the speech code. *Psychological Review*, *74*, 431–461.
- Mahon, B. Z., & Caramazza, A. (2003). Constraining questions about the organization and representation of conceptual knowledge. *Cognitive Neuropsychology*, *20*, 433–450.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: Structure and processes. *Current Opinion in Neurobiology*, *11*, 194–201.
- Martin, A., Ungerleider, L. G., & Haxby, J. V. (2000). Category specificity and the brain: The Sensory/Motor Model of Semantic Representations of Objects. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences*. Cambridge, MA: MIT Press.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, *379*, 649–652.
- Milner, A. D., Dijkerman, H. C., Pisella, L., McIntosh, R. D., Tilikete, C., Vighetto, A., & Rossetti, Y. (2001). Grasping the past: Delay can improve visuomotor performance. *Current Biology*, *11*, 1896–1901.
- Milner, A. D., Perrett, D. I., Johnson, R. S., Benson, O. J., Jordan, T. R., Heeley, D. W., Bettucci, D., Mortara, F., Mutani, R., Terazzi, E., & Davidson, D. L. W. (1991). Perception and action “visual form agnosia.” *Brain*, *114*, 405–428.
- Montomura, N., & Yamadori, A. (1994). A case of ideational apraxia with impairment of object use and preservation of object pantomime. *Cortex*, *30*, 167–170.
- Moreaud, O., Charnallet, A., & Pellat, J. (1998). Identification without manipulation: A study of the relations between object use and semantic memory. *Neuropsychologia*, *36*, 1295–1301.
- Mozaz, M., Rothi, L. J. G., Anderson, J. M., Crucian, G. P., & Heilman, K. M. (2002). Postural knowledge of transitive and pantomimes and intransitive gestures. *Journal of the International Neuropsychological Society*, *8*, 958–962.
- Muneaux, M., & Ziegler, J. C. (2004). Locus of orthographic effects in spoken word recognition: Novel insights from the neighborhood generation task. *Language and Cognitive Processes*, *19*, 641–660.
- Negri, G. A. L., Lunardelli, A., Gigli, G. L., & Rumiati, R. I. (in press). Degraded semantic knowledge and accurate object use in semantic dementia. *Cortex*.
- Ochipa, C., Rothi, L. J. G., & 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*, 374–381.

- Pinker, S., & Jackendoff, R. (2005). The faculty of language: What's special about it? *Cognition*, *95*, 201–236.
- Plaut, D. C. (2002). Granted modality-specific specialization in semantics: A computational account of optic aphasia. *Cognitive Neuropsychology*, *19*, 603–639.
- Pulvermuller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences*, *5*, 517–524.
- Rapcsak, S. Z., Ochipa, C., Anderson, K. C., & Poizner, H. (1995). Progressive ideomotor apraxia: Evidence for a selective impairment of the action production system. *Brain and Cognition*, *27*, 213–236.
- 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., Mack, L., & Heilman, K. M. (1986). Pantomime agnosia. *Journal of Neurology, Neurosurgery, and Psychiatry*, *49*, 451–454.
- 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., & Bekkering, H. (2003). To imitate or not to imitate? How the brain can do it, that is the question! *Brain and Cognition*, *53*, 479–482.
- 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.
- Schwartz, R. I., Barrett, A. M., Crucian, G. P., & Heilman, K. M. (1998). Dissociation of gesture and object recognition. *Neurology*, *50*, 1186–1188.
- Schwartz, M. F., Montgomery, M. W., Fitzpatrick-DeSalme, E. J., Ochipa, C., Coslett, H. B., & Mayer, N. H. (1995). Analysis of a disorder of everyday action. *Cognitive Neuropsychology*, *12*, 863–892.
- Seidenberg, M. S., & Tanenhaus, M. K. (1979). Orthographic effects on rhyme monitoring. *Journal of Experimental Psychology: Human Learning and Memory*, *5*, 546–554.
- Shiffrar, M., & Freyd, J. J. (1990). Apparent motion of the human body. *Psychological Science*, *1*, 257–264.
- Sirigu, A., Duhamel, J., & Poncet, M. (1991). The role of sensorimotor experience in object recognition. *Brain*, *114*, 2555–2573.
- Tanenhaus, M. K., Flanigan, H. P., & Seidenberg, M. S. (1980). Orthographic and phonological activation in auditory and visual word recognition. *Memory and Cognition*, *8*, 513–520.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., Fazio, F., Rizzolatti, G., Cappa, S. F., & Perani, D. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, *17*, 273–281.
- Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Science*, *5*, 244–252.
- Viviani, P., Baud-Bovy, G., & Redolfi, M. (1997). Perceiving and tracking kinesthetic stimuli: Further evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1232–1252.
- Viviani, P., & Stucchi, N. (1989). The effect of movement velocity on form perception: Geometric illusions in dynamic displays. *Perception and Psychophysics*, *46*, 266–274.
- Viviani, P., & Stucchi, N. (1992). Biological movements look uniform: Evidence of motor-perceptual interactions. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 603–623.
- Warrington, E. K., & McCarthy, R. (1983). Category specific access dysphasia. *Brain*, *106*, 859–878.
- Warrington, E. K., & McCarthy, R. (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.